

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 2017

SEPTEMBER 2, 1960

On the Trigemini Muscles of the Lizards *Xenosaurus grandis* and *Shinisaurus* *crocodilurus*

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INTRODUCTION

The main purpose of the present paper is to describe the masticatory muscles of two reptiles, the muscular anatomy of which is largely unknown owing to their rarity in collections. It is hoped that this investigation may provide clues concerning the relationships of the two genera represented as well as their relationships with other groups of recent saurians. The work of McDowell and Bogert (1954) deals with the systematic positions and relationships of these lizards, largely from evidence derived from external, skeletal, and sexual characters. My conclusions, based on only part of the musculature, are much narrower in scope.

On this occasion I wish to express my deep gratitude to Mr. Charles M. Bogert and his collaborators for their useful suggestions and help in connection with this work during my stay at the American Museum of Natural History during the winter of 1953 and 1954. I feel especially obliged to Mr. Bogert, who kindly invited me to dissect the very rare *Shinisaurus*, and added material of the fairly rare *Xenosaurus* as well, in order to enlarge the scope of my investigations. To Dr. S. B. McDowell I am deeply grateful for his painstaking editorial help.

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LIST OF ABBREVIATIONS

- A, tendinous raphe (see text)
"add. post.," adductor posterior-like part of adductor externus profundus
ang., angular bone
apo., aponeurosis between adductor externus medialis and adductor externus profundus
ap. or. lev. ang. o., aponeurotic origo of levator anguli oris
art., articular bone
B, tendinous raphe (see text)
B. ap., basal aponeurosis
b. v., blood vessel
C, tendinous raphe (see text)
c. c., m. constrictor colli
cer. mdb., m. cervico-mandibularis
cor., coronoid bone
den., dentary bone
d. m., m. depressor mandibulae
ecp., ectopterygoid bone
c. p., parietal eye
eptg., epipterygoid bone
erpl., external rictal plate
f., frontal bone
g., tendinous gutter (see text)
G. g., Gasserian ganglion
g. gl., m. genioglossus
ghy., m. geniohyoideus
gmy., m. geniomyoideus
ilgl., infralabial gland
ins. ap. 1b, insertional aponeurosis of part b of adductor externus superficialis
ins. B. ap., insertion of basal aponeurosis
irpl., internal rictal plate
jug., jugal bone
lev. ang. o. a, levator anguli oris a
lev. ang. o. b, levator anguli oris b
lev. b. a, part a of levator bulbi
lev. b. b, part b of levator bulbi
lev. b. d., m. levator bulbi dorsalis
lev. b. v. deep, deep portion of m. levator bulbi ventralis
lev. b. v. sup., superficial portion of m. levator bulbi ventralis
lev. ptg., m. retractor pterygoidei
lmc., ligamentum mandibulo-cutaneum
lqm., ligamentum quadrato-maxillare
lqm. fixed, fixed portion of ligamentum quadrato-maxillare
lqm. free, free portion of ligamentum quadrato-maxillare
mx., maxillary bone
myap., m. mylohyoideus anterior principalis
myas., m. mylohyoideus anterior superior
n. 1, 2, nerve of adductor mandibulae externus superficialis (1), and of adductor mandibulae externus medialis (2)

- n. my., superior nervus mylohyoideus
origo lev. ang. o. a, origo of levator anguli oris a
origo la, origo of part a of adductor mandibulae externus superficialis
ost., osteoderm
p., parietal bone
pofor., postfronto-postorbital bone
post. A, m. adductor posterior, anterior part
post. B, m. adductor posterior, posterior part
pot., proötic bone
pro. ptg., m. protractor pterygoidei
pseud. prof., m. pseudotemporalis profundus
pseud. sup., m. pseudotemporalis superior
ptg., pterygoid bone
ptgm., m. pterygoideus
qu., quadrate bone
sph. colli, m. sphincter colli
squ., squamosal bone
st. cl. mast., m. sternocleidomastoideus
sternohy., m. sternohyoideus
sur., surangular bone
T, tendinous ridge inside adductor mandibulae externus medialis separating
portion a from portion b
tab., tabular bone
tend. post. A, tendon of part A of m. adductor posterior
t. s., temporal aponeurotic sheet
tym., tympanic membrane
X, see text for explanation of this tendon
la, anterior part of m. adductor mandibulae superficialis
lb, posterior part of m. adductor mandibulae superficialis
lb ins., insertion of part b of adductor externus superficialis
lb post., adductor posterior-like subdivision of part b of adductor externus
superficialis
lb (α , β , γ), complex of subdivisions α , β , and γ of part b of adductor externus
superficialis
lb α , m. adductor mandibulae externus superficialis, part b, subdivision α
lb α ins., insertion of part b α of m. adductor mandibulae externus super-
ficialis
lb β , m. adductor mandibulae externus superficialis, part b, subdivision β
lb γ , m. adductor mandibulae externus superficialis, part b, subdivision γ
2a, part a of m. adductor externus medialis
2a ins., insertion of part a of m. adductor externus medialis
2b, part b of m. adductor externus medialis
3a, part a of m. adductor externus profundus
3a ant., anterior portion of part a of m. adductor externus profundus
3a deepest, deepest portion of part a of m. adductor externus profundus
3a ins., insertion of part a of m. adductor externus profundus
3a post., posterior portion of part a of m. adductor externus profundus
3b, part b of m. adductor externus profundus
3c, proötic head of m. adductor externus profundus
3c ins., insertion of proötic head of m. adductor externus profundus

3d, deep proötic portion of m. adductor externus profundus
V1, ramus ophthalmicus trigemini
V2, ramus maxillaris trigemini
V3, ramus mandibularis trigemini

REVIEW OF PREVIOUS WORK

The close relation of *Xenosaurus* with the Anguidae was stressed by Barrows and Smith in 1947, mostly on the basis of skeletal similarities. Previously Camp (1923) had employed several systems of organs in the comparative study on which he based his important classification of lizards. Camp concluded (p. 418): "*Xenosaurus* is specialized in throat musculature and loss of the third branchial arch, and is neither intermediate between the Anguidae and Iguanidae, nor related to the Gekkonidae. It is related to and probably derived from the anguids." The close relationship between *Xenosaurus* and *Shinisaurus* is stressed in the report by McDowell and Bogert cited above.

The few studies thus far made of *Xenosaurus* are in general agreement as to the placing of the Xenosauridae close to the Anguidae.

The position of *Shinisaurus* has remained obscure since the species was described by Ahl in 1930. Virtually nothing was known about the skeleton and the internal anatomy of this rare animal prior to the publication of the paper by McDowell and Bogert. Nopcsa (1932) briefly discussed the possibility of its relationships with *Lanthanotus* and *Heloderma*, now shown to be distantly related. Since Lakjer's (1926) comprehensive paper on the trigemini muscles of the Sauropsida, little has been done in this particular field as far as reptiles are concerned. Lubosch (1933) deals especially with the external muscles covering the trigemini group in different sauropsids, and there is the excellent work of Poglayen-Neuwall (1953a) on the trigemini muscles of *Sphenodon*. Unfortunately there are several errors in Lakjer's description of that form, especially his failure to note the presence of a well-differentiated levator anguli oris. Camp has demonstrated the importance of the external throat muscle pattern in his discussion of its phylogenetic and systematic implications. In dealing with this muscle group in both lizards here described, I have unavoidably duplicated some work on *Xenosaurus*, in comparing it with *Shinisaurus*. Oelrich's (1956) paper on the anatomy of the head of *Ctenosaura pectinata* was a welcome addition in this field of investigation.

McDowell and Bogert place *Xenosaurus* and *Shinisaurus* in separate subfamilies of the Xenosauridae, which comprise the diploglossan stock of the Anguimorpha together with the more primitive Anguidae and

the Anniellidae. Both genera in question have one cranial character in common, which is of the utmost importance in the differentiation of the jaw adductors, and in this point both differ strikingly from the other Diploglossa: the upper temporal fossa is relatively wide. In the anguid subfamilies Diploglossinae and Gerrhonotinae, the same fossa is considerably narrowed, and in *Ophisaurus* and *Anguis* (the subfamily Anguinae) it is restricted to a very narrow slit. However, in *Anniella* the upper temporal arch does not exist at all. I began this investigation expecting a rather close similarity between *Xenosaurus* and *Shinisaurus* owing to this expanded temporal opening. The facts prove that in spite of this similarity in the cranial muscles in general, and in the groups entering this fossa in particular, the differences are rather considerable. Even the arrangement of the fairly constant deeper temporal portions of the adductor and the constrictor internus dorsalis differs widely in both genera.

THE JAW MUSCULATURE OF *XENOSAURUS*

THE RICTAL PLATES AND LIGAMENTS EXTERNAL TO THE JAW MUSCLES

The external rictal plate (erpl.) forms a triangular tough infolding in continuation of the upper lip and extends as far backward from the posteroventral tip of the postorbital and suborbital bony frame as the latter is deep, just above its postmaxillary blunt prolongation (fig. 1). The rostral part of both rictal plates, the external and the internal, is hidden under the postmaxillary bony prominence formed by the juncture of the postfronto-orbital, the ectopterygoid, and the maxillary. The slanting dorsal margin of the plate, externally visible, is duplicated mesially, and in this way a triangular niche is formed between the external (erpl.) and internal (irpl.) plates. The latter is continued cranially as the lining of the lower lip.

The ligamentum quadrato-maxillare (lqm.) ascends from the mandibular articulation as a flattened, slightly arched tendon, the ventral border being slightly concave. At the point where it reaches its maximal height it splits in two branches. The deeper one is attached to the superficial fibers of the second portion of the adductor externus superficialis (1b) and reaches the posterior apex formed by the converging rictal plates, the "inner angle" of the mouth; the lateral branch of the ligament fans out into the skin of the anteroventral temporal region (lqm. free). The common posterior, arched portion of the ligament adheres to the upper border of the mandible in front of the mandibu-

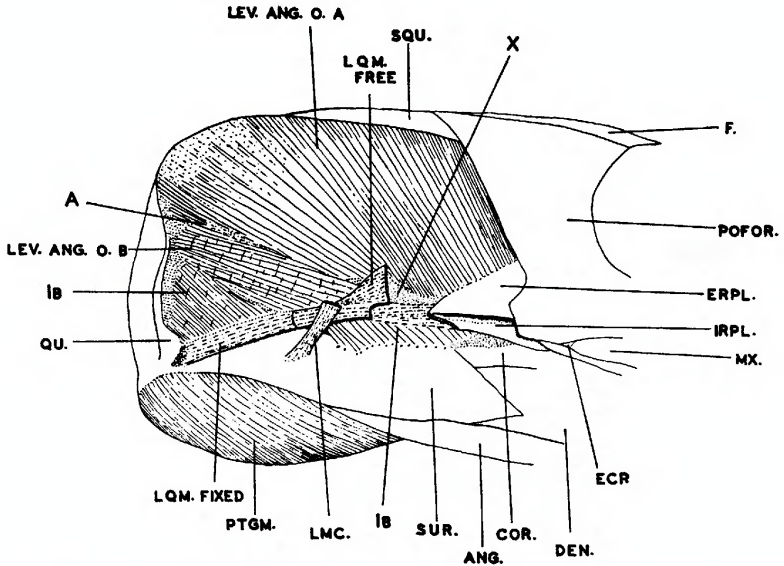


FIG. 1. The superficial layer of the adductores mandibulae of *Xenosaurus grandis*. The ligamentum quadrato-maxillare (lqm.) has been severed from its upper attachment with the skin and from its lower attachment with the rictal commissure (erpl. and irpl.). The lower ligament (lmc.) has been severed from its dermal attachment as well. Both parts of the levator anguli oris (a and b), representing adductor la, are visible, as well as a part of adductor lb and the submandibular belly of the m. pterygoideus (ptgm.). For tendons A and X, see text.

lar joint and seems at first glance to give insertion to superficial fibers of a muscle rising from the antero-external rim of the quadrate (lb). But, in fact, even the lateral fibers of this muscle are inserted on the upper border of the surangular.

A separate ligament (lmc.) rises at an angle of 45 degrees from the lateral surface of the surangular from a level of the middle of its depth and ends in the skin of the lower temporal region somewhat behind the attachment of the lateral branch of the ligamentum quadrato-maxillare. In overlapping this ligament it is fused with it at a point slightly behind the bifurcation; this central third of the ligamentum quadrato-maxillare has no connection with the upper border of the surangular; the adherent caudal third gives rise to a transparent aponeurosis covering a triangular area defined caudally by the vertical slope of the quadrate.

THE MUSCULAR SYSTEM

As in many other saurians the analysis of the jaw muscles is rather difficult, because the postorbital bar hides a large area of the most

anterior temporal musculature, and because of the imperfect separation of certain regions into clear-cut portions. Subdivisions by tendinous ridges and laminae make matters even more difficult. In the following description, Luther's and Lakjer's nomenclature of the trigeminus muscles is used, with some doubts and reservations, however, about its intrinsic value, especially in connection with the complicated array of subdivisions in the adductores externi group. The deeper portions, as defined by both authors, show a higher degree of individualization and constancy and are therefore much easier to define.

The profile views show a temporal area filled by musculature; the postorbital bar hides the anterior border of this bulging muscle mass. An approximately triangular area, narrowed ventrally, is covered by the flat postfronto-orbital bone. The posterolateral end of the mandible is slightly covered laterally by parts of the pterygoid muscle (fig. 1, ptgm.). The wide upper temporal aperture, completely filled with temporal muscles, exposes parts of two different adductors; their complex arrangement is discussed below.

SUPERFICIAL THROAT MUSCLES

Camp (1923, p. 369, fig. 60) gives a description and figure of the throat muscles of *Xenosaurus grandis*. The muscular arrangement of this area follows the relatively simple pattern in the Anguimorpha. I have repeated the same dissection and find full agreement with Camp's excellent drawing. There is, however, a slight deviation in the specimen at hand. The chin muscle typical for the Anguimorpha, Camp's geniomyoideus (gmy.), arises not from the mandibular rami proper but

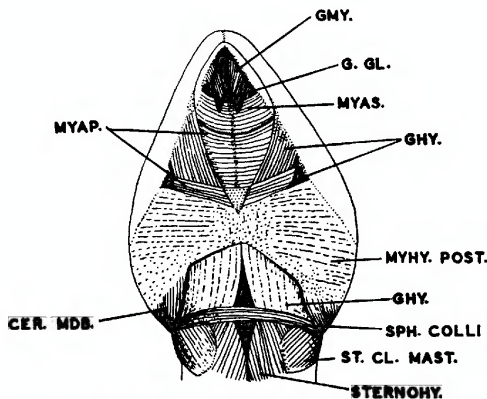


FIG. 2. The external layer of the throat muscles of *Xenosaurus grandis*. Camp's geniomyoideus muscle does not start directly from the ventromedian border of the mandible (splenius) but from an inscriptio tendinea of the genioglossus. Otherwise, compare with Camp's (1923) figure 60.

from a tendinous raphe almost parallel to and somewhat distant from the muscular attachment of the genioglossus. The mylohyoideus anterior superior (myas.) links both jaws in a caudally bulging arch, rather caudal to the main bulk of the geniomyoideus (fig. 2, gmy.). This different arrangement of the anterior transverse muscle (myas.) is certainly due to a different degree of contraction of this muscle, but the difference in attachment of the geniomyoideus seems to be of more importance, because all the other drawings of Anguinea in Camp's paper show this muscle as arising from the mandible proper (in *Xenosaurus*, *Heloderma*, *Gerrhonotus*, and *Anniella*).

ADDUCTOR MANDIBULAE GROUP

Luther divides this muscle group as follows:

A. Adductor mandibulae externus, lateral to the rami infraorbitalis and mandibularis trigemini.

B. Adductor mandibulae internus, medial to both of these nerves.

C. Adductor mandibulae posterior, caudal to these nerves, especially in relation with the n. mandibularis, and also medial to the n. mandibularis ("always," see Lakjer, 1926, p. 52).

In certain cases, the adductor posterior is not well separated from the profundus portion of the adductor mandibulae externus (deepest portion of the latter, 3 in Lakjer's figures). The ramus cutaneus nervi mandibularis forms in such cases a good borderline between the two portions. In our particular case, the degree of individualization of muscles increases laterally to medially. In other words, to describe first the more conspicuously separated deeper adductor portions seems more practical.

ADDUCTOR MANDIBULAE INTERNUS: In *Xenosaurus*, this group consists of three muscles: the m. pterygoideus, and two partly coherent muscoli pseudotemporales, distinguished as the lateral pseudotemporalis superior and the medial pseudotemporalis profundus. In this respect *Xenosaurus* does not differ from the majority of the other saurians.

The pseudotemporalis superior (figs. 8, 10-13, pseud. sup.) rises from the lateral border of the parietal as far as it delimits the upper temporal fossa and fills, as seen from above (fig. 8), more than the median half of the surface of this elliptic perforation. This muscle has a very considerable transverse thickness in its dorsal part but flattens considerably towards its insertion. The fleshy belly ends approximately at the level of half of the depth of the temporal region. Posterior and external fibers converge upon the medial side of an aponeurosis that also re-

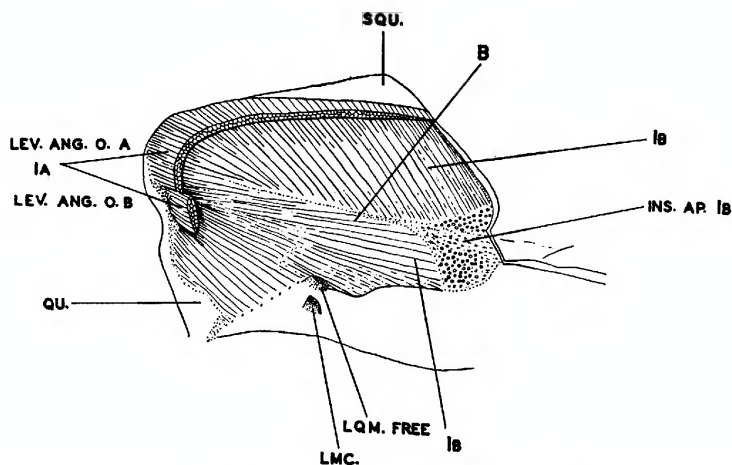


FIG. 3. *Xenosaurus grandis*. Both ligaments have been removed together with both parts of the levator anguli oris (origo preserved), exposing raphe B of lb fused to triangular aponeurosis dorsally and ventrally (bipinnate muscle).

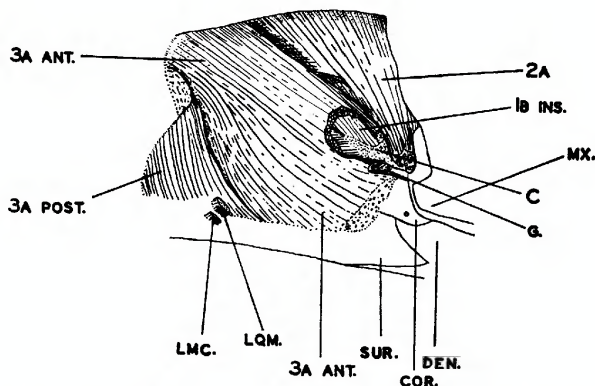


FIG. 4. *Xenosaurus grandis*, showing the insertion of the deep dorsal pinna and fibers of the ventral pinna of portion lb at the raphe C, which bends outward, forming a gutter (g.) ending externally as the raphe B. Ventral parts of lb have been removed.

ceives fibers from the adductor externus medialis (dorsally) and from the adductor externus profundus 3b (dorsocaudally). Deeper rostral fibers at the inner side of this aponeurosis are the longest. Closely adjacent to, but nevertheless well separable from, the anterior border of the deeper pseudotemporalis profundus, they reach the coronoid process almost up to its summit. The caudal part of the insertional aponeurosis covers directly the anterior ventral half of the m. pseudotemporalis profundus. In a dorsal direction, this aponeurosis is gradually freed

from the pseudotemporalis profundus, and its medial detached surface collects posterior fibers of the pseudotemporalis superior. By this arrangement, only the foremost bundles of the pseudotemporalis superior insert, almost without an interposed tendinous lamina. The aponeurosis, which may be compared with Lakjer's "*Bodenaponeurose*," transmits the vertically adducting pull of the pseudotemporalis superior to the sloping posterior ridge of the coronoid bone at the inner side of the mandible. The posteroventral area of this aponeurosis adheres only to the surface of the deeper muscle, without collecting any of its fibers.

The m. pseudotemporalis profundus (pseud. prof., figs. 11-13) has an almost triangular contour and covers the epipterygoid bone completely. In being expanded near its insertion, it is in one respect just the opposite of the pseudotemporalis superior, which tapers towards the mandible and has a very much elongated origin. The restricted area of origin of the deeper muscle covers a small area of the membranous lateral wall of the brain case in front of and above the dorsal end of the epipterygoid near the end of the anterodorsal wing of the proötic. This rather narrow upper end of the muscle expands fanwise ventral to the ophthalmic and maxillary rami of the trigeminus (V1 and V2), which bridge both pseudotemporales at a rather high level in relation to the full height of the temporal area. The long insertional area starts at the summit of the coronoid bone. From there, it follows the inner sloping caudal ridge and continues medial to the entrance of the third branch of the trigeminus into the mandible on a bony ledge of the "compound bone" under this foramen up to a point halfway between the trigeminal foramen and a lateral prominence in front of the articulation with the quadrate. In this way, the third branch of the trigeminus overlaps this muscle laterally in its arched course towards the mandible. This is the only adductor without any aponeurosis or tendinous ridge; therefore its fibers form an undisturbed, regular, fanwise-flattened belly with a somewhat bulging anterior slope, covered in a gutter-like way by the anterior, long-fibered part of the pseudotemporalis superior. The whole arrangement of this muscle group resembles the pattern figured by Lakjer (1926, fig. 163) for *Lacerta ocellata* in relative form and size of both parts and in relation to the ramus mandibularis trigemini. But in *Lacerta* an insertional tendinous mirror collects a good deal of the caudal part of the pseudotemporalis profundus.

The m. pterygoideus (ptgm., figs. 7-9, 11-14) has a rather normal shape, similar to that of most saurians, in being represented by a single, cushion-like muscle which protrudes at the posterolateral surface of the

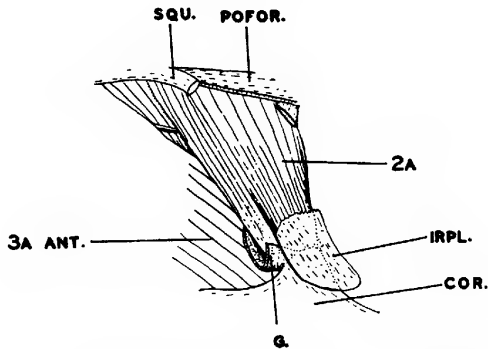


FIG. 5. *Xenosaurus grandis*. The gutter (g.) formed by the fusion of raphe B and C after removal of the insertion of the 1b shows the insertion of deeper 2a bundles at its base and at the tip of the coronoid, whereas lateral ones (compare fig. 4) end at the inside of the inner rictal plate. The slanting fibers medial to the gutter belong to the adductor externus profundus (3a ant.).

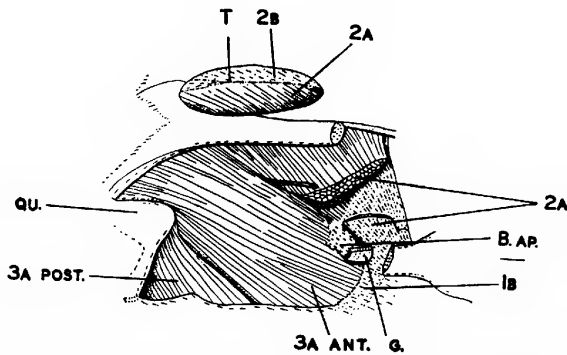


FIG. 6. *Xenosaurus grandis*. An oblique dorsal view showing the penetration of both adductor externus medialis portions (2a and 2b) into the temporal aperture. Parts of 2a near the insertion are removed in order to show the deeper 2b, more or less parallel with 3a ant.

mandible. Here it envelops the processus retroarticularis laterally, posteriorly, and medially and fills a slight insertional scar at the ventrolateral surface of the compound bone, avoiding the angular. At this level (fig. 14) the belly of the muscle swings around the ventral border of the mandible and forms a long fleshy insertion at the ventrolateral ridge of the pterygoid bone, just reaching the lateral corner of the ectopterygoid. The insertion, seen in profile, does not follow a straight line. The posterior tip of the pterygoid bone, in front of the junction with the quadrate, remains free of muscular attachment. The most caudal insertional fibers reach in a limited area the lateral border of the m. protractor pterygoidei (fig. 14). The insertional border then

slopes downward to the lateral border of the pterygoid bone, keeping clear of the epipterygoid-pterygoid articulation and following the external, arched border of the pterygoid. No indication of a deep pterygoideus accessorius muscle could be found.

ADDUCTOR MANDIBULAE POSTERIOR: In the special case of *Xenosaurus*, this muscle is not clearly delimitable from the partly parallel adductor mandibulae externus profundus, at least in its medial parts (fig. 9, "add. post."). It is not laterally bridged over by the ramus mandibularis trigemini as in most of the snakes, in *Varanus*, or in certain saurians. The cutaneous branch of the ramus mandibularis, the other criterion for the separation of the adductor mandibulae posterior from the adductor externus profundus, could not be traced.

In spite of these difficulties, a small, triangular muscle might be considered as a much-reduced adductor posterior (fig. 9). It rises from the anteromedian, almost vertical edge of the quadrate that is formed by the angulated juncture between the anterior, transverse conch with the vertical, sagittal blade of this bone. The insertion extends, in a dorsocranially curved line, from a point just in front of the mandibular joint to the summit of a knob-like prominence of the slightly higher median wall of the dorsally fluted compound bone (fig. 9). In the specimen at hand this dorsomedian spur was much more developed than in the specimen figured by Barrows and Smith (1947). This reduced adductor posterior is laterally and medially enclosed by fibers of the complex adductor externus profundus; the whole, very flattened, muscle is fleshy. The innervation pattern, however, does not demonstrate that this muscle is a real adductor posterior, because it should, generally speaking, be innervated from a branch in common with the mm. pseudotemporales and pterygoideus. Such is certainly not the case here. The "add. post." shown in our illustrations is innervated together with portions belonging to the adductor externus profundus (3 of Lakjer's figures). It is therefore possible that a portion of this muscle mimics exactly the position and morphological independence of a vanished, earlier, real adductor posterior. We therefore face a certain dilemma. We may consider this muscle as a functional substitute of an adductor posterior, but, according to its innervation in adductor externus style, it seems proved that *Xenosaurus* has, *de facto*, no adductor posterior. In this respect, *Xenosaurus* deviates considerably from the normal saurian patterns, but is not alone in this respect, as amphisbaenids and *Lialis* (*vide* Lakjer) likewise have no adductor posterior. For convenience, the name "adductor posterior" should be maintained but in quotation marks.

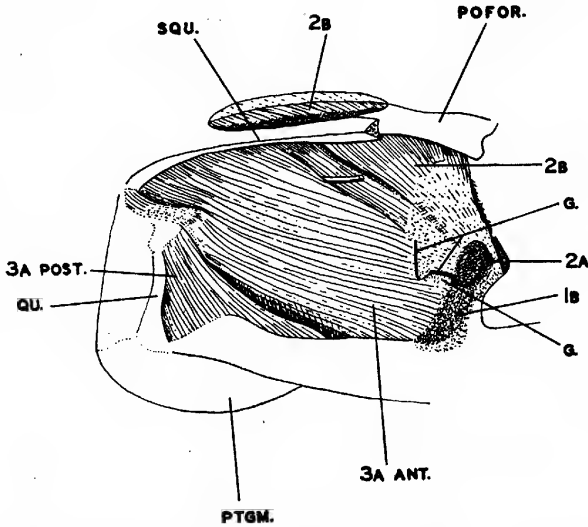


FIG. 7. *Xenosaurus grandis*. After removal of 2a, the deep medialis 2b is exposed; it fills the medial half of the temporal aperture. The insertion of 2a (inner part) and the ventral part of 1b on marginal parts of the coronoid are seen. Two distinct portions of the adductor externus profundus (3a ant., 3a post.) are visible.

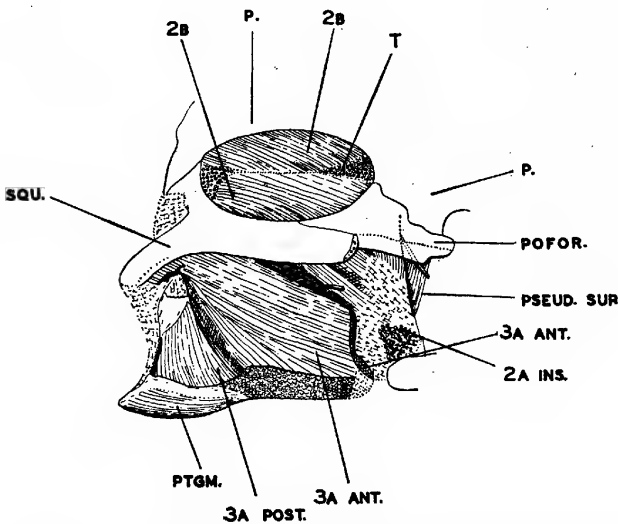


FIG. 8. *Xenosaurus grandis*. Oblique dorsal view of upper temporal opening and (lower) temporal area, showing 2b as a whole. In front of this muscle, a small part of the m. pseudotemporalis superior (pseud. sup.) is seen. This figure stresses the fact that marginal (= lateral) fibers of 3a ant. insert at the inside of the covering fascia. The steeply fibered triangular muscle rising from the quadrate is a 3a post. Dorsal fibers of 3a end at the aponeurotic plate at the lower end of 2b (cut stump is shown).

ADDUCTOR MANDIBULAE EXTERNUS: Lakjer divided this group of muscles into three portions (superficialis, 1; medialis, 2; and profundus, 3), but this division is manifest only in a relatively limited number of forms among the sauropsids. In many (but not all) snakes, three portions are clearly in evidence. In saurians and *Sphenodon*, portion 3 is double-headed, and as a rule many accessory differentiations occur. For example, a levator anguli oris, derived from the adductor externus superficialis, may be present. In contrast, incomplete separations in the frame of these three "acknowledged" portions complicate matters to a high degree. In the case of *Xenosaurus*, subdivisions and incomplete splitting hamper any attempt at an adequate description.

Adductor Mandibulae Externus Superficialis (1): A thin sheet of fibers rises from the ventral border of the squamosal posteriorly to a point near the contact of this bone with the quadrate (figs. 1, 3). From this region and the external ridge of the quadrate, a tendinous band develops which slopes towards the inner angle of the mouth, forming a narrowly triangular wedge; it may be called A. This structure is continued caudoventrally as a transparent sheet extending from the lateral border of the quadrate to the fixed caudal third of the ligamentum quadrato-maxillare (fig. 1, short vertical lines intersecting the posteroventral muscle fibers). This membrane does not gather any muscular fibers but forms the ventral continuation of the faintly bipartite levator anguli oris. The caudal part of this muscle (lev. ang. o. b) rises from the tendon-capped area of the upper quadrate joint and ends at the inner side of the free stretch of the ligamentum quadrato-maxillare. The much bigger, fan-like, anterior portion of the muscle (lev. ang. o. a) covers two-thirds of the temporal surface and is hidden at its sloping cranial border by the broad postfronto-orbital. This bone gives rise to no fibers of this muscle. This cranial portion ends ventrally at the upper ridge where the external rictal plate bends back and forms the internal rictal plate. Fibers ending in a tendinous mirror (X in fig. 1) medial to the free portion of the ligamentum quadrato-maxillare follow caudally. This mirror is connected in front with the rictal plates. The above-mentioned tendinous spur, A, does not form a clear-cut separation between the two parts of the levator anguli oris; rostroventrally, the separation becomes blurred by fibers crossing the tendinous division. As a levator anguli oris, we may call this muscle, following Lakjer, a part of 1a.

The most ventrocaudal fibers seen in figure 1 (1b) in front of the mandibular joint must be considered as parts of a deeper portion of the adductor externus superficialis, 1b; this part has no relation to the

rectal area. The insertion area visible under the unattached part of the zygomatic ligament close to the rictal region belongs to the same muscle. Figure 3 demonstrates, after removal of the rictal plates and the caudally adherent aponeurosis with all the external parts of 1a inserting on these structures, the continuity of the two parts of 1b visible in figure 1. The separation of 1a from the deeper layer 1b is clear near the angle of the mouth, but becomes rather vague as one proceeds in a dorsocaudal direction, following the tendinous streak A. The deeper layer, 1b (fig. 3), contains near its rostroventral end an aponeurotic surface, continued as a tendinous spur which may be called B, parallel to and deeper than the superficial spur A but somewhat more dorsal. The most caudal and ventral fibers of 1b are the steepest; they reach the upper-lateral insertion line at the mandible directly. Gradually, more rostral and dorsal fibers converge towards B or the insertional aponeurosis near the caudal border of the coronoid process. In a similar way, dorsal fibers rising from the squamosal enter the same raphe and aponeurosis B, duplicating the laterodorsal levator anguli oris in this area. A pinnate arrangement results, with the ventral hemipinna partially and gradually deviated to the mandible. The separation between the dorsocaudal parts of 1a and 1b becomes rather arbitrary towards the posterodorsal corner of the temporal region, above the dorsal head of the quadrate. Fibers cross over from layer to layer, but ventrally the different insertions separate the two parts.

Lakjer gives a rather similar arrangement of the adductor externus superficialis for *Ophisaurus*. In *Xenosaurus*, the ventral part of 1b inserts along a wavy line at the dorsolateral edge of the compound bone. The remainder of 1b converges into B, which, triangularly expanded, transfers the pull to the border of the processus ascendens of the coronoid.

Muscle 1b duplicates the external layer in its bipinnate arrangement. The adductor externus superficialis consists of a bipinnate external muscular sheet in connection with the rictal region (1a = levator anguli oris), and a deeper adductor, 1b, with a wide insertional edge along the upper edge of the mandible from the articular area to the posterior border of the coronoid elevation. The separation of the two muscles is most clear in the insertional regions, but is blurred dorsally. Some difficulty arises if we try to delimit the anterior border of 1b and if we try to find a clear separation from the more or less parallel lateral parts of the complex adductor externus profundus (3). After the complete removal of 1a, the insertional aponeurosis of 1b is seen (fig. 3, ins. ap. 1b). This is a diamond-shaped field that collects fibers medially and

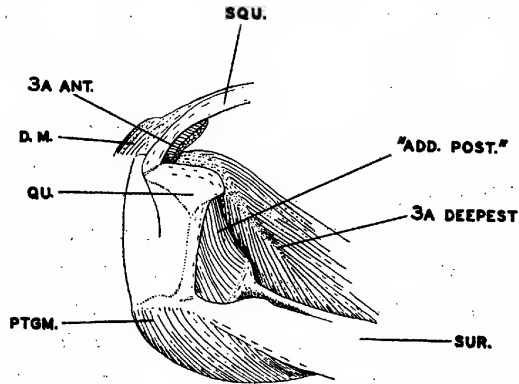


FIG. 9. *Xenosaurus grandis*. Detail after removal of 3a post., showing the internal tendinous spur inside the innermost part of the adductor externus profundus 3a post. The fibers arising from the vertical slope of the quadrate exhibit similarity to an adductor posterior ("add. post.," see p. 12).

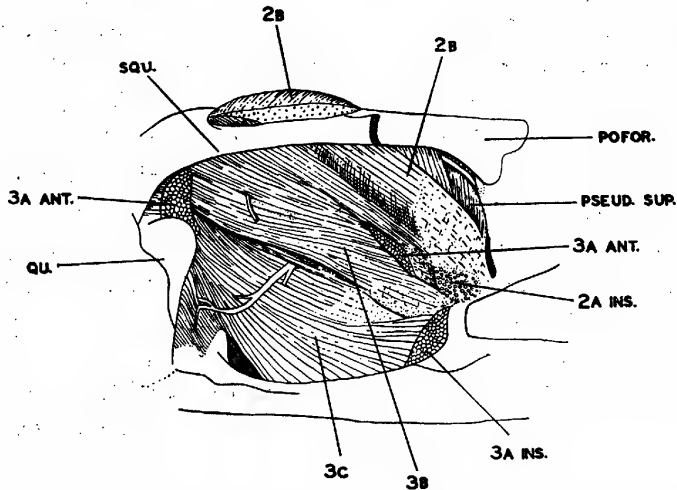


FIG. 10. *Xenosaurus grandis*. Lateral view after removal of 3a (both ends left *in situ*). The fusion of parts of 3b with 2b is evident. The n. adductor externus profundus shows the common innervation of 3c with the questionable more external and posterior "add. post." The nerve does not split the muscle mass into clearly separable portions.

at its borders. It is continued caudally as the raphe B, which collects fibers from both sides, along the lower border at a low angle, and from above at a much steeper one. The resulting bipinnate fiber arrangement is, therefore, asymmetrical. The dorsal group is transversely thin at the anterior end and very thick towards the posterodorsal corner of the temporal region. This considerable muscle mass originates mainly

from the internal surface of the squamosal, mostly from the divergent parts overlying the upper quadrate joint. The anteroventral fibers of this dorsal half of 1b enter the inner surface of the lozenge-shaped aponeurosis, restricted to a triangular area. A much larger triangle collects anterior fibers of the ventral compartment in a similar way.

After the dorsal half of the pinnate 1b is removed (compare figs. 4 and 5), a clear separation between 1 (adductor externus superficialis) and 2 (adductor externus medialis) is seen, formed by a deeper and shorter tendinous raphe of a more dorsal level than B, but connected with the latter anteroventrally. This juncture produces a gutter-like structure, g. This deep raphe collects a deeper array of the double-layered dorsal half of 1b; this large portion covers the posterior three-quarters of the temporal area. At the anterior slope of this portion, the separation between 1b, the deeper 3a, and the lateral adductor externus medialis (2a in figs. 4, 5) is visible and is stressed by the n. adductor externus superficialis (n. 1, 2). The anterior quarter of the temporal area is filled by the steeply fibered fraction of the medialis. This separation between 1b and 2 can be followed in a posterodorsal direction, as it gradually becomes stronger and more conspicuous.

In summary, there are two main components to the adductor mandibulae externus superficialis. One is the lateral levator anguli oris, subdivided by the raphe A. The upper expanded part of this muscle (lev. ang. o. a, fig. 1) fills the whole lateral aspect of the ventral border of the temporal arch and extends cranially beyond the postorbital bar; the posteroventral portion (lev. ang. o. b, fig. 1) is much smaller. The second component, deeper layer 1b, converges into a tendinous mirror at the posterior slope of the coronoid (fig. 2, ins. ap. 1b). From here raphe B develops at a slightly higher level than A, but with a parallel slope. The bipinnate arrangement of 1b is further complicated by a double-layered dorsal half. The external layer rises from the whole length of the upper temporal arch and ends in the raphe B and, dorso-cranially, in the insertional mirror. The deeper layer does not extend quite so far cranially and ends at the deeper tendinous spur C (fig. 4), dorsomedial to B. Raphe C converges ventrally with B, forming a gutter (g.), V-like in transverse section. The outer layer of the adductor externus medialis, 2a, exposed in the anterior part of the temporal area after removal of the lateral layer of the dorsal 1b (figs. 4 and 5), inserts inside this gutter. I consider all fibers converging into the outer blade of this gutter, lateral to the insertion of 2a, as well as all the slanting fibers collected by the inner blade of the gutter, parts of the deep superficialis 1b. All parallel deeper fibers medial to this gutter must be

considered parts of a similarly complex and subdivided adductor externus profundus (3). (Compare figs. 4 and 5.)

Adductor Mandibulae Externus Medialis: Lakjer had many difficulties in separating the adductor externus profundus (3) from more lateral portions. He defines (p. 31) the "basal aponeurosis" [*"Bodenaponeurose"*] as the limiting surface; all fiber systems inside this plane belong to the profundus; all lateral fibers represent deep portions of the superficialis (1) and medialis (2).

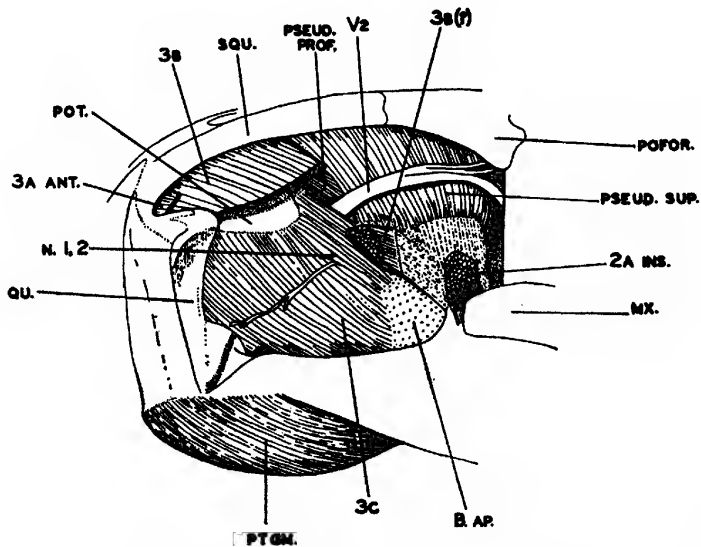


FIG. 11. *Xenosaurus grandis*. A central part of portion 3b has been removed along with the deepest fibers of "add. post." (a portion of m. adductor externus profundus), giving a view of the basal aponeurosis (B. ap.), collecting 3b, 3c, and the pseudotemporalis group. At this stage, the pseudotemporalis superior only (pseud. sup.) is exposed. 3c rises from the proötic insertion of 2b at the top of the coronoid process.

Often matters are not quite so clear as this simple scheme seems to imply, because exact delimitation and definition of the basal aponeurosis are not always possible. In the case of *Xenosaurus*, this structure (see below) is of moderate size and fuses at its anterior border with a parasagittal tendinous incription separating an outer, lateral (2a) from a medial (2b) belly of the adductor externus medialis by reaching the surface of the upper temporal fossa (figs. 6–8). Both portions fill exclusively the temporal aperture. The most external and longest fibers of the lateral belly 2a reach the upper posterior border of the processus

coronoideus (figs. 5-7). Seen in profile, both portions have a triangular shape. One side of this triangle is situated in the level of the temporal opening. The posterior side is longest, and the anterior slope encloses with the upper side an angle of about 120 degrees. The nerve of the adductor medialis lateralis clearly separates the medialis (2) from the parallel caudal profundus (3) fibers which, however, rise from the under side of the squamosal (3a ant. of figs. 5 and 7). In figure 6 the complicated insertion of the lateral part of the medialis is shown. The most cranial fibers, attached in part to a lateral tendinous plate (part

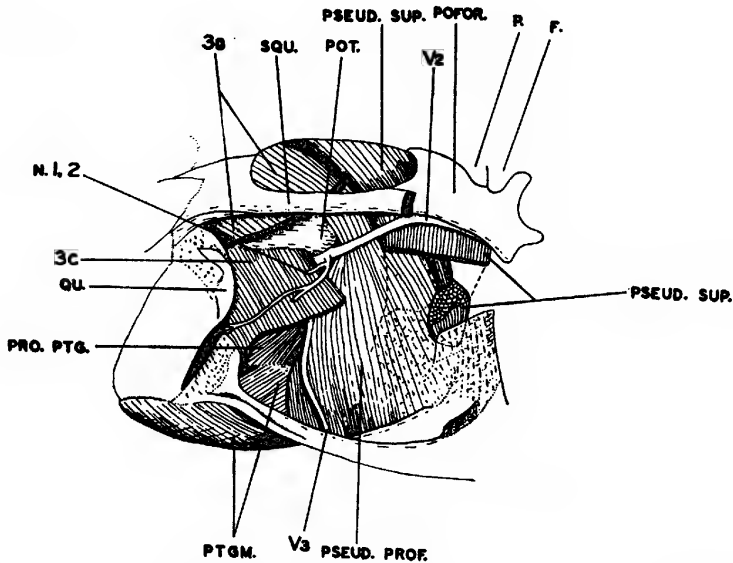


FIG. 12. *Xenosaurus grandis*. The ventral part of 3c and a central fraction of the pseudotemporalis superior have been removed in order to show the huge pseudotemporalis profundus (pseud. prof.). 3b and the pseudotemporalis group penetrate the upper temporal opening but are completely covered by the origins of the adductor externus medialis (2a and 2b). A hatched line shows the contour and extension of the insertional aponeurosis of pseudotemporalis superior.

of the tendinous, "diamond-shaped" anterior end of tendon B), reach the uppermost part of the posterior slope of the coronoid directly. More posterior fibers are transformed into a short, insertional, flattened tendon which enters the gutter formed by fusion of raphe B with raphe C. Raphe C, however, converges into the basal aponeurosis (fig. 6, B. ap.) The lateral medialis is partly removed in figure 7, showing the insertional stump and the flattened, triangular cross section. This

portion is, in contrast to the medial one, long-fibered and starts from tendinous structures only, such as the parasagittal spur at the dorso-lateral and dorsal surface of the deeper portion. The deeper portion (2b) rises from the medial border of the temporal fossa, formed by the parietal. The deeper medialis exhibits at its lateral and ventral part a considerable tendinous expansion, which collects the ventrally tapering muscle mass at its anterior and postero-caudal circumference. This aponeurosis forms a part of the "*Bodenaponeurose*," as it receives on its inner side the pseudotemporalis system (see p. 10). The posteroventral angle of this aponeurosis collects a part of the rostral insertional fibers of the lateral fraction of the adductor externus profundus (3a, figs. 7-9). We see, therefore, that this basal aponeurosis splits into individual aponeuroses for the different temporal muscles.

Adductor Mandibulae Externus Profundus: The adductor profundus is the most complicated muscle of the adductor group. In order to gain an idea of its configuration, it seems advisable to give an enumeration of its integral parts, proceeding from inside laterally.

A proötic portion (3c) pierced by branches of the n. adductor externus 3, rises from a peculiarly bent area on the lateral surface and the anterior border of the proötic (3c, fig. 11). At the anterior slope of the muscle the ramus maxillaris trigemini emerges. This thin muscular sheet (3c) starts caudally well inside the slope of the quadrate. The anteroventral part of the insertion at the inner flange of the fossa primordialialis of the mandible is tendinous and adheres to the insertion of the double m. pseudotemporalis (3c, figs. 10-12). This connection, however, is restricted to the anterior third of the muscular belly, which ends at the posteroventral border of the basal aponeurosis. From the upper margin of the aponeurosis, the pseudotemporales, especially the pseudotemporalis superior, fan out. Figure 11 shows the main posterior part of the proötic head of the profundus entering the primordial fossa.

Several end aponeuroses of other muscles that also end at the lateral surface of the basal aponeurosis have already been mentioned. One not yet discussed is the aponeurosis of portion 3b, the second main division of the externus profundus. The second part of the profundus, corresponding with Lakjer's 3b, rises from the posteroventral surface of the caudal part of the squamosal (figs. 10-14). Towards the insertion, its fibers converge into a tendinous sheet from its medial surface. Part of this sheet reaches (fig. 11) the basal aponeurosis, and part the posterior slope of the coronoid.

More lateral fiber systems rising from the posterior half of the squamosal (3a ant., fig. 8) fill the anterior half of the mandibular inser-

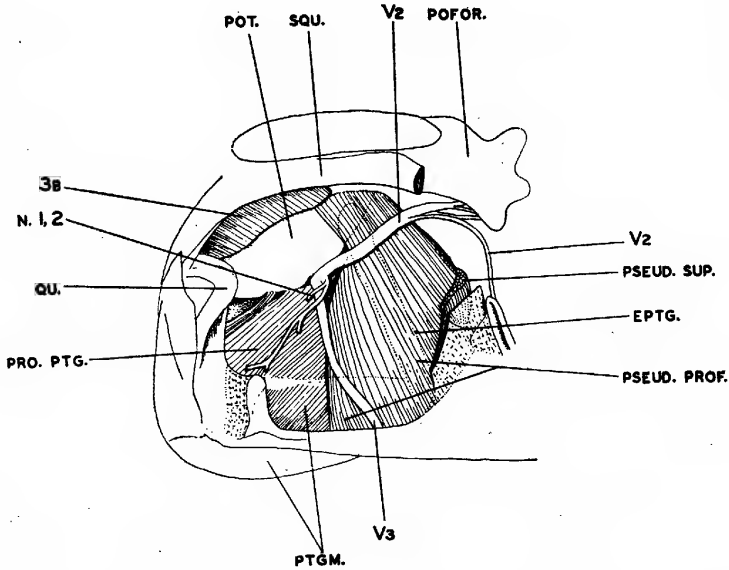


FIG. 13. *Xenosaurus grandis*. 3c and the pseudotemporalis superior are removed, in order to show the protractor pterygoidei (pro. ptg.) and the origo of the m. pterygoideus. A line of dots indicates the contour of the epipterygoid (eptg.).

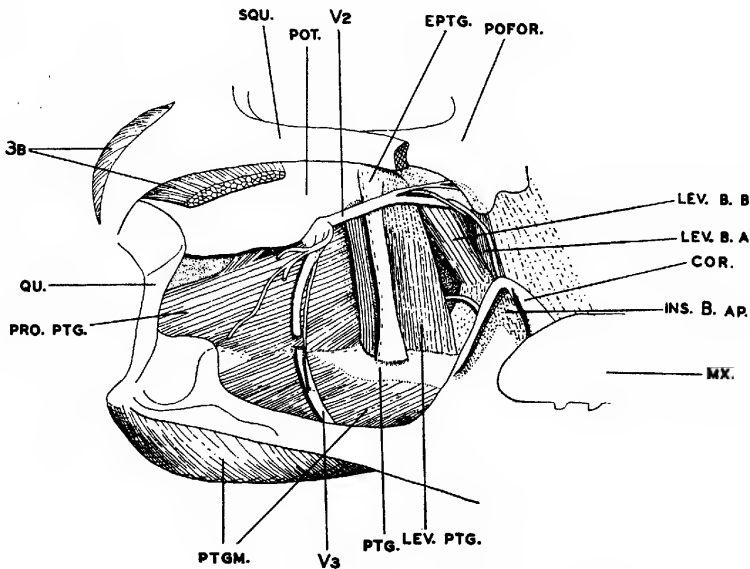


FIG. 14. *Xenosaurus grandis*. View of the whole constrictor internus dorsalis: a bipartite levator bulbi (lev. b. a, lev. b. b), a levator pterygoidei inside the epipterygoid (lev. ptg.), and a "bicipital" origin of the protractor pterygoidei (pro. ptg.) are seen. Note the separate innervation of the m. pterygoideus.

tional groove, with the exception of the most cranial fibers which are caught by the covering fascia (this area is indicated by closely packed circlets) near the posterior border of the coronoid. Near the origo, a tendinous hood covers the upper end of the quadrate; this structure is enclosed in this slanting muscle, which may be termed 3a.

Another portion of the adductor externus profundus (3a post., figs. 7, 8) develops from the whole anterior slope of the quadrate and inserts in the posterior half of the groove on the upper surface of the compound bone. This portion of the profundus is overlain laterally by parallel fibers of the superficialis (1b), but the 1b fibers rise from the posterior part of the temporal arch from areas above the quadratum, which is strictly avoided.

This summary description of the profundus gives only a faint idea of all the complicated structural details, which concern mostly the portions 3a, 3b, and the triangular caudal part descending from the quadrate. Comparison of figures 6 through 12 will give an idea of the intricate details. In addition the emerging motor branch for this muscle splits off some fiber bundles in a position somewhat intermediate between our 3b and the proötic head. Such a portion may be seen in figure 11 above the emerging trigeminus branch for the profundus; it fills the gap between the deep medialis (2b) and 3b and rises from the under side of the posterior border of the temporal opening. Dorsally it is partly fused with this medialis portion, but ventrally it is closely connected with the proötic head of the profundus; it should be considered a deeper part of 3b (figs. 11-13, pierced by the trigeminal branch for add. 1 and 2, n. 1, 2).

In *Xenosaurus*, in association with the flat and wide posterior part of the skull and the wide temporal openings, the adductor externus system reaches a high degree of subdivision. All these portions, with the main exception of the levator anguli oris and caudal elements, converge towards the coronoid and the postcoronoid area of the mandible. Most of these portions, especially the cranial ones, insert in a rather crowded way at and near the posterior slope of the coronoid prominence. Here they are restricted to tendinous sheets merging in the basal aponeurosis which extends at the level of the m. pseudotemporalis profundus and the proötic head of the adductor externus profundus. All lateral temporal muscles are attached more or less to this aponeurosis by tendinous sheets or spurs. These again cause both splitting and peculiar partial fusions of elsewhere well-separated muscles. Even portions like the adductor externus medialis and profundus may show such fusions (see above).

CONSTRUCTOR INTERNUS DORSALIS SYSTEM

The following portions can be distinguished: The flattened, rather feeble *m. levator pterygoidei* (fig. 14, lev. ptg.) extends medial to the epipterygoid. Its longitudinally developed insertion at the roof of the pterygoid bone extends more in front than behind the epipterygoid. The main direction of the fibers indicates a slight retracting pull on the pterygoid. The origo area comprises caudally the anterior end of the proötic wing, and cranially a slanting line of attachment from the membranous wall of the brain case. This anterior part is reduced to a tendinous sheet; caudal fibers start directly from the proötic without undergoing any subdivision.

This muscle covers the origo of the extensive protractor pterygoidei (fig. 14, pro. ptg.). A very slight subdivision, better termed an isolated bundle, rises from the middle of the lower border of the proötic. The main bulk rises from the basisphenoid and the processus basalis. The insertion, at the dorsal surface of the posterior half of the pterygoid, starts somewhat craniomedial to the posterior contour of the levator and ends at the caudal tip of the bone. The oblique fibers indicate a strong pull of the pterygoid in a craniodorsal direction.

The protractor bulbi group consists of two separate portions. A bigger caudal fan rises from the membranous brain case, partly medial, partially cranial, to the origin of the levator pterygoidei. A thin, steeper bundle is overlapped ventrally by the posterior portion and rises from a more cranial limited area of the brain case (fig. 14, lev. b. a). Both bundles converge ventrally upon a slightly postorbital area of the lining of the roof of the mouth. Perhaps the caudal muscle levator bulbi b can be homologized with Lakjer's levator bulbi ventralis, and the other with the dorsalis. The general arrangement of this group corresponds fairly well with the conditions figured by Lakjer (1926, pl. 2, fig. 7) for *Ophisaurus*, but I could not find any suborbital prolongation of the fibers of the levator bulbi dorsalis. Both end at the same closely circumscribed area.

This description of the trigeminal muscles of *Xenosaurus* is followed by a parallel report of the conditions found in *Shinisaurus*, which differs from the former species in many ways. In this connection it should be remembered that *Xenosaurus* has a rather flat and wide skull and an extremely well-developed temporal opening. *Shinisaurus*, however (see McDowell and Bogert, 1954, figs. 4, 5), has a rather highly built, narrow skull with fairly wide but more elongate temporal openings. It is evident that such striking differences in general proportions should be linked with considerable differences in the muscular differentiations.

THE JAW MUSCULATURE OF *SHINISAURUS*

THE RICTAL PLATES AND LIGAMENTS EXTERNAL TO THE JAW MUSCLES

During the first steps of the preparation of the jaw musculature the wide postorbital bar, formed mostly by the jugal, hampered the exact delimitation of the anterior border of the superficial temporal muscles. In order to trace this rostral slope of the muscle mass, the dorsal part of this bone had to be removed. The suture between the postfronto-postorbital and the jugal was severed and the ascending ramus of the jugal was filed across (compare figs. 17 and 19). Another difficulty lay in the presence of a tough aponeurosis covering the upper temporal aperture, anchored laterally between a series of enlarged osteoderms and the bones of the temporal arch. This series of accessory ossifications had to be removed gradually during the course of the preparation.

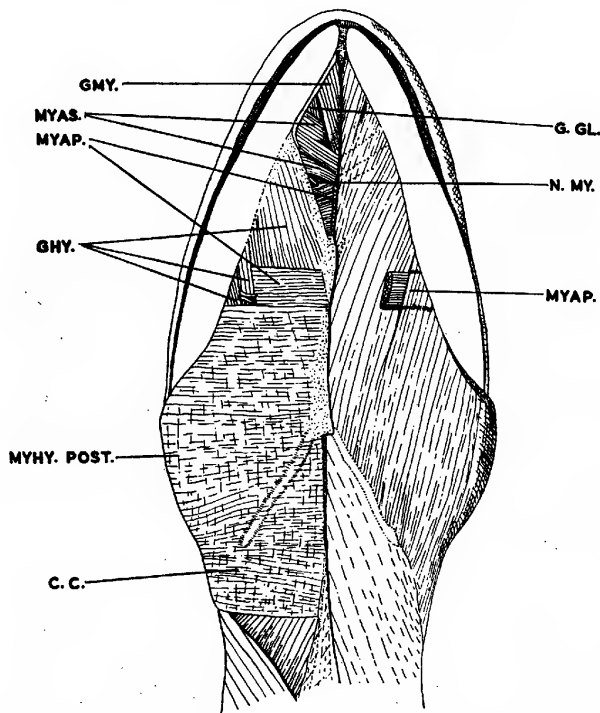


FIG. 15. *Shinisaurus*. Superficial (left) and deeper (right) layers of the throat muscles. The relatively simple pattern of interdigitations between the mylohyoideus (myap. and myas.) and geniohyoideus (ghy.) systems, and the presence of a geniomyoideus (gmy.), are both characteristic anguimorph features. At the right half of the figure the contours of the external muscles have been superposed (in stippled lines) on top of the deeper layer.

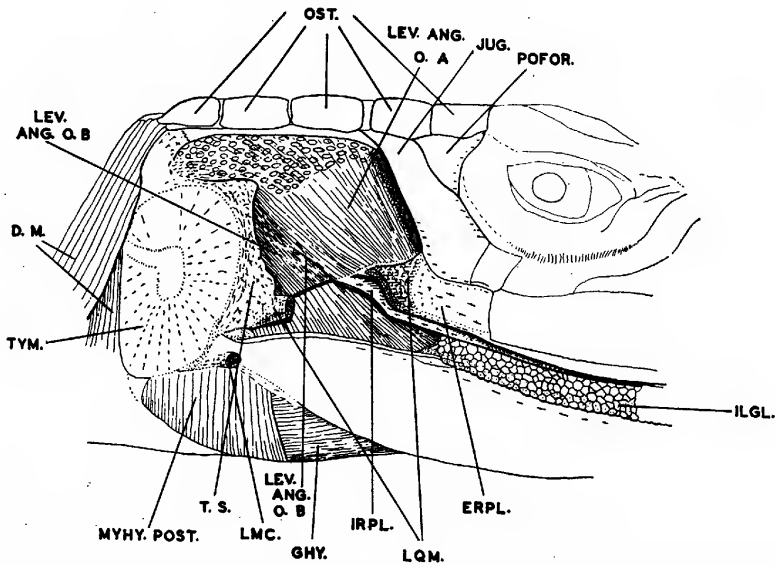


FIG. 16. *Shinisaurus*. External layer of the temporal area. The free portion of the ligamentum quadrato-maxillare (lqm.) and the lower mandibulo-cutaneous ligament (lmc.) to the skin have been severed. Both portions of the levator anguli oris (lev. ang. o. a and lev. ang. o. b) are visible; ventrally, portion 1b extends to the mandible.

They are more or less rectangularly bent in cross section, with a horizontal and a vertical blade meeting at a canthal ridge superposed on a corresponding ridge along the temporal arch.

The skin of the lower temporal region is connected by a short ligament (fig. 16, lmc.) to the mandible in front of the anteroventral edge of the extensive, vertically elliptical, tympanic membrane (tym.) Another close attachment of the skin is seen at the external rictal plate (erpl.) behind the posterior end of the maxillary bone. The lower border of the ligamentum quadrato-maxillare (lqm.) is free and clearly visible after the removal of the skin. There is no substantial glandular tissue along the upper lip, but an elongate infralabial gland (ilgl.) lines the lower dental series, starting somewhat in front of the rictal commissure. The external rictal plate is closely attached to the posterior supralabials. The dorsal border of the ligamentum quadrato-maxillare is continued as a tendinous sheet that gradually merges with the skin in the anterodorsal temporal region. Caudally, this sheet (t. s.) becomes gradually tougher and extends, freely movable, across the anterior frame of the quadrate for the tympanic membrane and forms its tendinous middle layer. This direct continuation of the temporal fascia into the core of the tympanum is remarkable. Only at the dorsal rim

is the tympanic membrane closely affixed to the upper head of the quadrate. The quadrato-maxillary ligament broadens in the vertical direction from its posterior end at the lower end of the vertical slope of the quadrate towards the external rictal plate (erpl.) in a wedge-like shape. Along the oblique dorsal border of the anterior third of the ligament, the internal rictal plate (irpl.) bends ventrally, covering the anterior muscular slope of the jaw muscles towards the mandible. The ligamentous structures of the lateral temporal region in *Shinisaurus* differ strikingly from those of *Xenosaurus*. In *Xenosaurus* the main ligament ends at the angle between both rictal plates and emits a postcommissural branch which fans out into the skin behind the angle of the mouth. The origin of the posterior mandibulo-cutaneous ligament (fig. 1, lmc.) has a considerably more cranial position, and the posterior half of the ligamentum quadrato-maxillare is not free, but fused with the upper margin of the compound bone of the mandible. (Compare fig. 1 and fig. 16.)

THE MUSCULAR SYSTEM SUPERFICIAL THROAT MUSCLES

Camp shows that the differentiation of the external throat muscles in saurians presents data useful for our inferring the systematic relations between families. Similarly, he shows the relative constancy of certain morphological traits for systematic units larger than families. All the characteristics elaborated by Camp for the Anguioidea agree closely with the conditions found in *Shinisaurus*. There exists a dis-

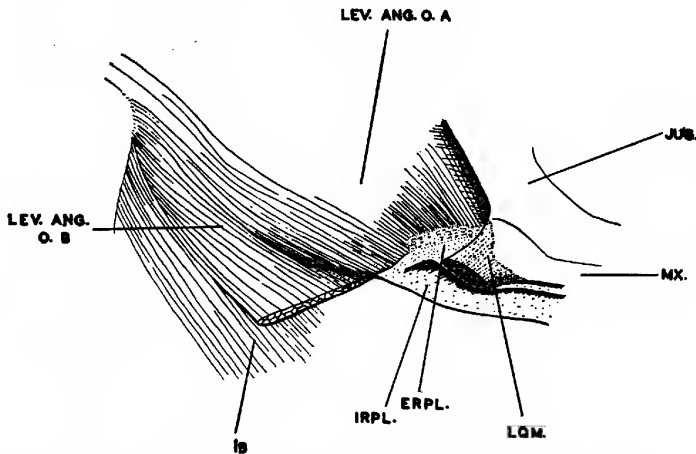


FIG. 17. *Shinisaurus*. Detail, showing the relations of both parts of the levator anguli oris to the rictal area.

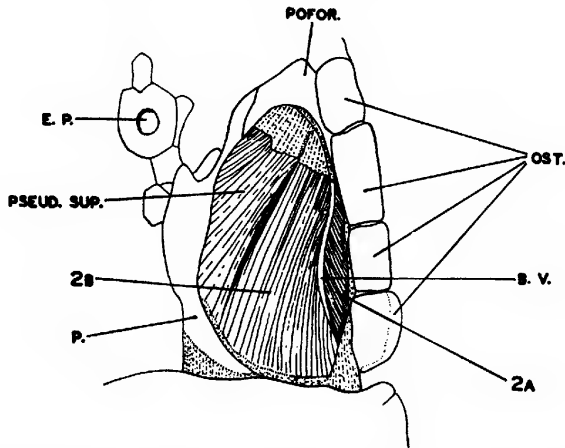


FIG. 18. *Shinisaurus*. Dorsal aspect of the right upper temporal aperture, exposing the two partitions of the pseudotemporalis superior. Compare with figure 23.

tinct geniomyoideus muscle, well separated from the deeper genioglossus (fig. 15, gmy.). The mylohyoideus splits into four distinct portions, and only a few interdigitations take place between the geniohyoideus and mylohyoideus muscles. This situation corresponds fairly well with the conditions in *Xenosaurus*. There are, however, some minor differences between the genera. First, the whole intermandibular area is rather slender in *Shinisaurus* compared with the greater inter-ramal angle in *Xenosaurus*. The geniomyoideus has no posterior sagittal attachment to the skin of the intermandibular angle, but it is covered caudally by a posterior slip of the mylohyoideus anterior and reaches not the skin, but rather the common ventro-sagittal raphe. The cervico-mandibularis, instead of being set off from the mylohyoideus posterior as in *Xenosaurus*, is fused in *Shinisaurus* with a rather conspicuous sphincter colli (figs. 2 and 15).

ADDUCTOR MANDIBULAE GROUP

ADDUCTOR MANDIBULAE INTERNUS: The pseudotemporalis group shows the normal division into a superior and profundus portion as in most saurians (figs. 18, 29, 30, pseud. sup. and pseud. prof.). The pseudotemporalis profundus is rather small, well isolated from the superior. The profundus is a transversely flattened, narrow muscle (fig. 30, pseud. prof.) with a posterior dorsal tendinous seam which has its origin on the inner side of the articulation between the uppermost corner of the proötic and the dorsal end of the epipterygoid. Shorter, and more

rostral, fibers originate from the lower half of the posterior slope of the epipterygoid. The insertions occupy a dorsomedial ridge at the middle area of the composite bone. This small muscle is completely hidden laterally by the pseudotemporalis superior.

The slight development of the pseudotemporalis profundus contrasts strikingly with the condition found in *Xenosaurus*, in which the muscle expands towards its insertion strongly in a parasagittal plane, whereas in *Shinisaurus* the muscle has the form of a band with parallel anterior and posterior borders. In *Xenosaurus*, the length of its insertion is almost triple the length of the origo. Even this latter area expands from the anterodorsal corner of the ala proötica beyond the upper articulation of the epipterygoid to a considerable field of attachment at the membranous covering of the brain in front of the columella. The whole of the epipterygoid is completely hidden by the profundus, as seen laterally (figs. 12, 13). In *Shinisaurus*, the epipterygoid is completely exposed, and the muscle is restricted to a narrow zone just behind it. There are some attachments at the posterior border of the bone itself and a very slight dorsal extension medial to it. With regard to this muscle, the differences between the genera are very striking.

The m. pseudotemporalis superior is a very extensive muscle of trapezoid shape (fig. 30, pseud. sup.). The insertion covers an area from the top of the posterior slope of the coronoid to the anterior half of the composite bone, as far backward as the posterior border of the pseudotemporalis profundus. The muscle is crossed laterally by the second and third trigeminal branches at different levels. In front of the ala proötica there is a trough-like excavation on the outer surface of the muscle into which fit parts of the adductor externus. The maxillar branch of the trigeminal nerve follows this gutter-like surface closely (fig. 30, V2). The origin is rather shorter than the long insertion and starts at the medial suture between the postfronto-postorbital and the parietal. More posterior fibers rise from the membranous lateral wall of the brain case, and the most caudal ones rise from the anterior tip of the ala proötica. The origo of this muscle is visible also from the upper side of the temporal fossa. The pseudotemporalis superior fills the anteromedian half of the temporal opening (figs. 18, 23), whence it rises from the parietal exclusively. The last, caudal fraction of this bone, as far as it forms the periphery of the aperture, gives rise to parts of adductor medialis fibers. This margin of attachment is the dorso-external limit of a much wider and expanded area of origin, as can be seen in the lateral views of the muscle in figure 30 and the description

of the origin above. An invasion of this muscle into the temporal opening is known from other saurians, in which this gap is wide, as in *Tropidurus* and *Calotes* (Lakjer, 1926, figs. 63, 64). In the anguid *Ophisaurus apodus* the fossa is very much reduced and therefore not invaded by temporal muscles. The portion of this muscle in front of the lateral trough-like depression is strongly thickened transversely, but the anterior border forms a wedge-like sharpened edge. A tendinous mirror collects a great many of the most anterior, external fibers that converge towards the upper part of the posterior slope of the coronoid; the fibers following insert directly. A good many of the deeper fibers of the caudal part of the muscle rise from the caudal border of the lower half of the epipterygoid, followed by the externally visible proötic attachments and preceded by attachments from the membranous side wall of the brain case. From here the field of origo covers the anteromedian part of the temporal fossa with a prolongation to the inner (ventral) suture between the parietal and the postfronto-postorbital.

A comparison of *Shinisaurus* with *Xenosaurus*, concerning the relation between both components of the pseudotemporalis group, shows that in *Shinisaurus* a very large superficialis overlaps the slender profundus, which is restricted to the posterior area of the combined muscle group (fig. 31, pseud. prof.). In *Xenosaurus*, a rather slender and anteroposteriorly reduced pseudotemporalis superior overlaps some-

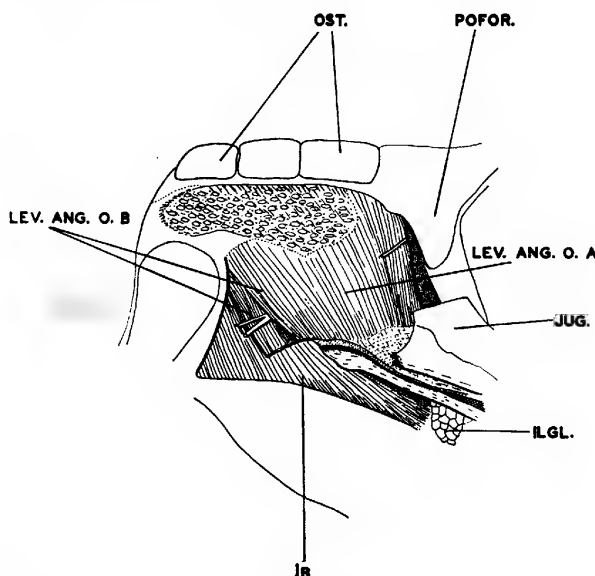


FIG. 19. *Shinisaurus*. Compare this more complete view with figure 17.

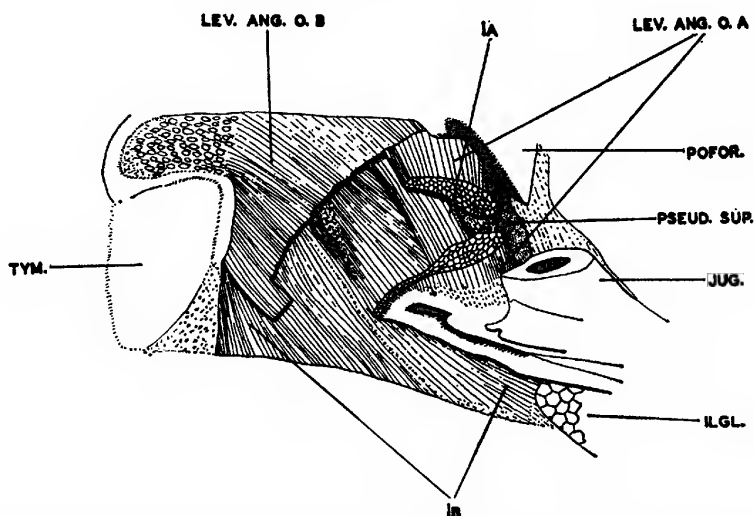


FIG. 20. *Shinisaurus*. Parts of the postorbital bar (upper half of jugal) have been removed, thus exposing the anterior slope of the adductor area formed by (partly removed) levator anguli oris a, which is thickened at its rostral slope. Part of the posterior part of the levator has been removed. Under this muscle two parts of the adductor externus superficialis (*sensu stricto*) 1a and 1b, are visible.

what less than the anterior half of the enormous pseudotemporalis profundus. But in other details (anterolateral tendinous mirror, anterior insertion at the coronoid slope), there is a certain similarity between the genera. In *Shinisaurus*, a small part of the pseudotemporalis superior muscle bulges into the anteromedian part of the temporal opening, whereas in *Xenosaurus* the whole upper part of this muscle is tucked under the medial (parietal) border of the fossa. The very extended origo covers the anterior three-quarters of the median circumference of the opening, but without being seen from above. As in *Xenosaurus*, the lateral tendon of the pseudotemporalis superior is an integral part of Lakjer's "*Bodenaponeurose*," which collects from its posterior margin slanting fibers of the 3b portion of the externus group. But this aponeurosis is partly coalesced with the surface of the pseudotemporalis profundus in *Xenosaurus*. In other words, in the latter genus the posteroventral part of the pseudotemporalis superior is not fleshy and is attached to the fascia of the pseudotemporalis profundus over a considerable area. In *Shinisaurus*, both muscles have broad, fleshy insertions, with the only exception being at the anterolateral margin of the pseudotemporalis superior. The dorsally expanded pseudotemporalis superior, narrowed towards its insertion as in *Xenosaurus*, covers a wide pseudotemporalis profundus, and thus

corresponds nicely with Lakjer's (1926) figures 154 and 155 of *Varanus bengalensis*. To a lesser degree, there is agreement with his figure 165, representing *Calotes emma*, and his figure 164, representing *Zonurus giganteus*. A reduced pseudotemporalis profundus, combined with a huge pseudotemporalis superior, as is seen in *Shinisaurus*, seems to be a novelty for a saurian.

The m. pterygoideus (figs. 21, 22, 25, 30-32, ptgm.) has the normal saurian structure and is not subdivided. In the lateral aspect, a fairly large part of the subarticular and postarticular region of the mandible is enveloped and encircled by this muscle. It swings around the ventral border of the posterior part of the mandible and has a fairly expanded insertion at the lateral border of the pterygoid. As in *Xenosaurus*, the posterior end of the pterygoid is free of attachments of this muscle but the slope of the insertional fibers is stronger than in *Xenosaurus*. The entrance of the nerve separates this muscle superficially into three successive but coalescent insertional areas of approximately equal size. This fission, however, does not split the muscle as a whole (see fig. 32). Such subdivision is not seen in *Xenosaurus* (fig. 14).

ADDUCTOR MANDIBULAE POSTERIOR: As in *Xenosaurus*, there are deep, well separable parts of the adductor mandibulae externus profundus (3) that rise from the anteromedian surface of the quadrate and may be considered a reduced adductor posterior (figs. 28, 29, post. A, post. B). The muscle is represented by two distinct parts. The deeper part (post. A) rises from a very restricted area at the inner side of the angular transition of the upper head of the quadrate into the "body" of that bone. This flattened tendon expands ventrally and emits a long, flattened, muscular sheet of rather short fibers. The elongate insertional line starts in front of the mandibular articulation and ends cranially just behind the entrance of the ramus mandibularis trigemini into the lower jaw. The lateral and posterior part of this muscle (post. B) is completely fleshy and links the anterior slope of the quadrate with a small area at the immediate anterior surface of the mandibular joint. The fibers rise from the lower two-thirds of the quadrate and reach the articular area at a much steeper angle than shown by the fibers of the anterior part. As in *Xenosaurus*, this portion duplicates the deepest caudal parts of the adductor externus profundus and is perhaps only an internal part of this muscle. Nothing can be found, however, in *Xenosaurus* corresponding to the deep adductor posterior (post. A) of *Shinisaurus*. The author believes that this part A only may be a true but reduced adductor posterior, in spite of the more cranial course of V3.

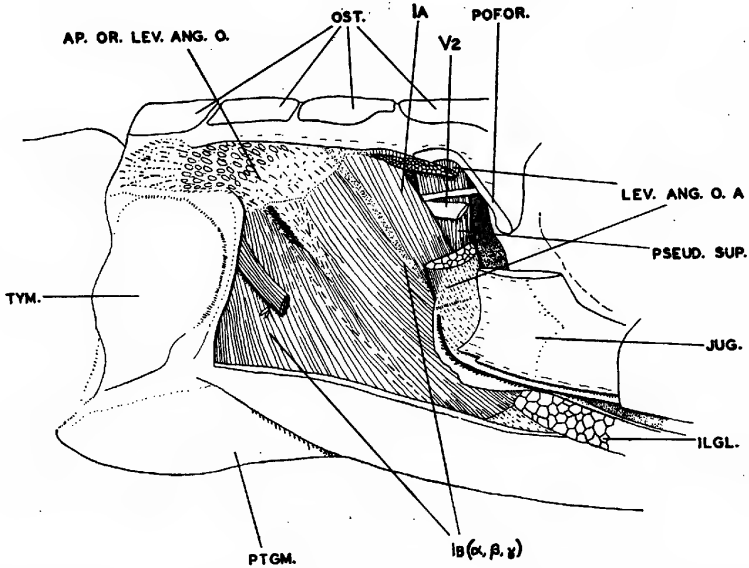


FIG. 21. *Shinisaurus*. More of the levator anguli oris has been removed (parts of the most anterior and posterior extension left *in situ*). The 1a-1b complex with its complicated tendinous spurs is seen. Rostrally, parts of pseudotemporalis superior (pseud. sup.) are visible. For details, see text.

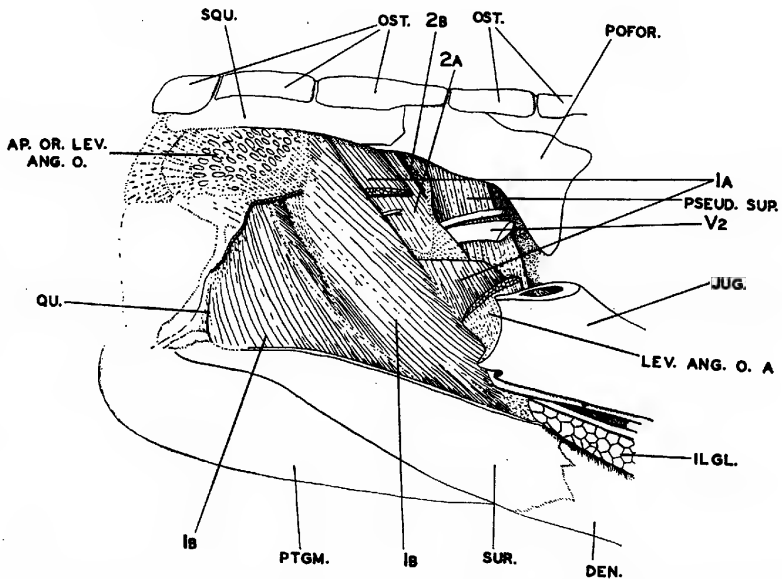


FIG. 22. *Shinisaurus*. Parts of the upper, easily separable portion 1a of the adductor externus superficialis have been removed, exposing a fraction of the lateral adductor externus medialis 2a. This figure repeats the features of the composite 1b.

ADDUCTOR MANDIBULAE EXTERNUS: The external layer of the adductor mandibulae externus superficialis is, at the rostral part of the temporal muscle mass, differentiated as a levator anguli oris which more caudally is a thin sheet of fibers independent of the rictal area (figs. 16, 17, 19, 20, lev. ang. o. a and lev. ang. o. b). The levator rises from the inside of an aponeurosis which bridges the gap between the upper border of the quadrate and the lateral rim of the temporal arch. This muscle tapers cranially and ends at the base of the postorbital bar. The deepest fibers of the levator anguli oris rise directly from the dorsomedian border of the temporal arch together with the aponeurosis. The anterior fibers of this muscle, which end at the ridge between the external and internal rictal plates, are steeper than the posterior ones. Fibers that follow caudally are somewhat less steep (lev. ang. o. b) and end in a sloping plane that reduces into a transparent aponeurosis. This aponeurosis connects with the skin and with the posterior, annexed part of the ligamentum quadrato-maxillare, as well as with the muscle. The same membrane has anterior connections with the much tougher internal rictal plate. This plate collects the rostral two-thirds of the levator anguli oris, here described as portion a, at the rictal commissure. The part of the muscle rises only from the above-mentioned aponeurosis but inserts directly on the rictal plate. The posterior thin portion b is somewhat overlapped by portion a.

The anterior slope of the quadrate gives off fibers [1b (α , β , γ)] parallel with levator anguli oris. The levator anguli oris, however, does not belong to the adductor mandibulae externus superficialis (1) proper. We may, therefore, repeat that the separate levator anguli oris is bipartite in the anteroposterior sense, with insertion at the temporal skin caudal of the rictal area. This insertional aponeurosis is overlapped by the free dorsal branch of the ligamentum quadrato-maxillare. The hindmost fibers of 1b anterior rise from the posterior border of the origo aponeurosis of portion 1a. The most caudal fibers of 1b posterior are the steepest and diverge strongly from those of the posterior border of portion 1a, the fibers of which grow steeper towards the anterior border of this portion, until they parallel the posterior fibers of 1b. The emergence of two small cutaneous nerves stresses the gap between both successive portions of 1b (fig. 20). A horizontal cut across the levator anguli oris group reveals that the muscle (a) has its maximal thickness near the steeply fibered anterior margin near the insertion at the rictal commissure; here the muscle shifts somewhat under the posterior border of the jugal (fig. 20). This anterior bulky part rises from the inner surface of the postfronto-postorbital.

But it is not quite feasible to subdivide this rather complex levator anguli oris into clear-cut portions, as is done above in a preliminary way. The thick anterior part thins out caudally, and the most anterior insertions at the rictal commissure indicate that at least this part is a typical levator anguli oris (a). More or less coherent posterior fibers detach themselves from the rictal region and pass into the above-mentioned thin aponeurosis which ends in the temporal skin. But a small caudal part of this thin b portion (fig. 20) is clearly separated by (1) its steepest fibers, (2) the intervening two caudal nerve rami, and (3) a

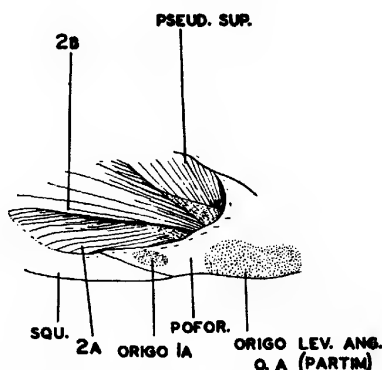


FIG. 23. *Shinisaurus*. Detail of upper temporal opening, showing the three muscles (2a, 2b, and pseudotemporalis superior, inside the fossa), and indicating the origo areas of levator anguli oris a (*partim*) and the restricted origo of 1a from the under side of the postfronto-postorbitale.

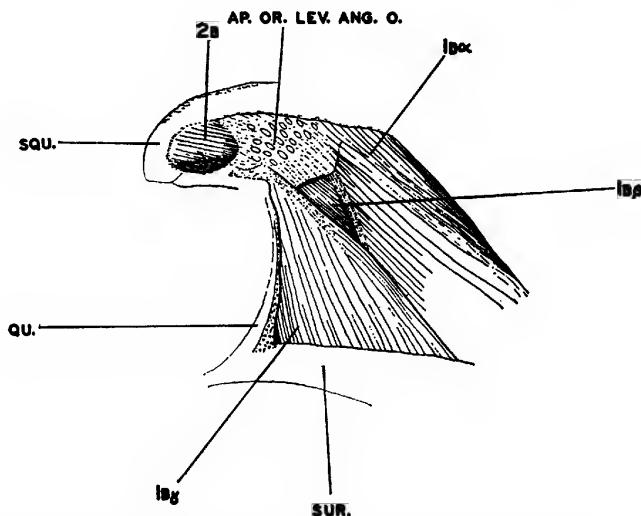


FIG. 24. *Shinisaurus*. The subdivisions of 1b (1ba, 1bβ, 1bγ).

caudal, separate origin from the middle of the dorsal margin of the quadrate where it meets the origo aponeurosis of levator anguli oris a. This caudal fiber group joins the same thin insertional aponeurosis with b and does not reach the mandible. It belongs, therefore, to portion b of the levator anguli oris (figs. 21, 22). It should be stressed that the whole posterodorsal part of this muscle becomes very thin, until it ends at the aponeurotic mirror between the upper end of the quadrate and caudal parts of the exteroventral border of the temporal arch. From the posterior part of this aponeurosis fibers develop which belong to a different muscle, the adductor externus superficialis proper (1). This common tendinous origin is manifest only after the levator anguli oris is removed; then the small bundle from the inside of the quadrate is clearly seen. The anterior thickened part arises mostly from the under surface of the postfronto-postorbital (fig. 23) but fails to bulge into the lateral part of the upper temporal fossa.

Adductor Mandibulae Externus Superficialis (1) Sensu Stricto: All parts of this muscle group follow a more or less parallel direction [1a, 1b (α , β , γ), fig. 21] in anteroposterior succession but not without partial fusions. The most cranial subdivision (1a) rises from a small, well-defined area on the under side of the wedge-like end of the postfronto-postorbital, which forms part of the temporal arch (fig. 23, origo, 1a). This area corresponds in profile view (fig. 21, 1a) to a point opposite the posterior half of the longest osteoderm in the series closely adhering to the temporal arch (the third counted from caudal to rostral). This rather narrow portion of the muscle has parallel anterior and posterior borders and reaches a ridge at the anterior slope of the coronoid bone, and cranially reaches even to the hindmost spur of the dentary. It is partly fused with the fascia at the anterior slope of the portion that follows. A tendinous raphe marks the line of fusion. This anterior portion of adductor 1, which may be called 1a, is better defined than the following part 1b.

Subdivision 1b has its origin in a posterodorsal area at the inside of the superficial aponeurosis stretched across the corner between the posterior part of the temporal arch and the upper head of the quadrate. This is the same aponeurosis that gives off at its anteroventral border the thin caudal portions of the levator anguli oris (see above). Portion 1b develops not only from the upper part of this aponeurosis but also from an oblique tendinous spur of which the apex points rostroventrally (figs. 22, 24) and enters, in a pointed, wedge-like fashion, the posterodorsal two-thirds of the lateral surface of 1b. The anterolateral portion of 1b thus set off inserts directly at the upper, anterior half of

the border of the surangular and at the posterior margin of the ascending part of the coronoid, but most of the fibers of this muscle insert indirectly on the surface of a deeper tendinous extension of a similar insertional area. In this way a very enlarged deep insertional surface is provided ($1b_{\alpha}$ ins., fig. 25). It should be stressed that this deep

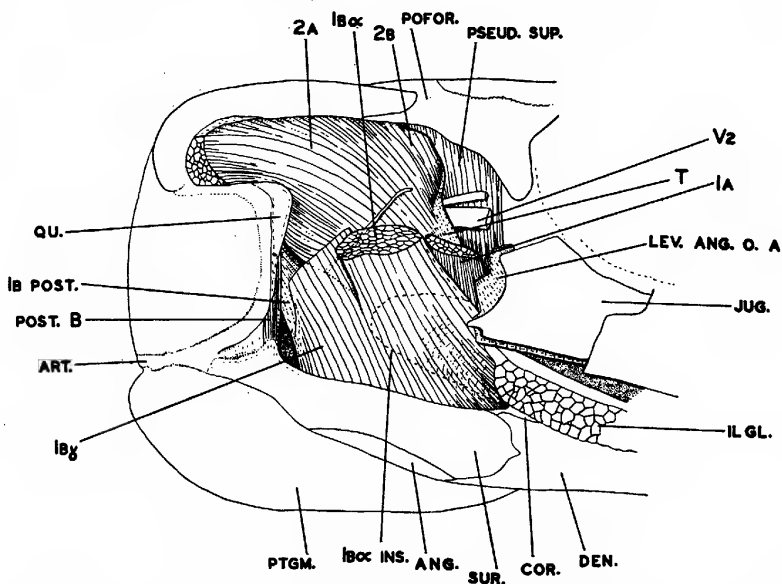


FIG. 25. *Shinisaurus*. Dorsal parts of 1a and 1b have been removed in order to show the adductor externus medialis (2a and 2b) and the m. pseudo-temporalis superior (pseud. sup.). A hatched line circumscribes a projection of the insertion of $1b_{\alpha}$ at the surface of the basal aponeurosis. The adductor-posterior-like deep portion of 1b (here marked 1b post.), which is interposed between two presumed true adductor posterior portions (post. B here visible), emerges from the interior slope of the quadrate.

tendinous structure collects both medial and lateral portions of the adductor externus medialis (see below) and at its posterolateral and medial surfaces also collects a number of different adductor portions converging towards the angle between the posterior slope of the processus ascendens coronoidei and the upper ridge of the surangular. It has, therefore, the characteristics of Lakjer's "Basal" or "Bodenaponeurose." The exterocaudal portion of the 1b part of this muscle (γ) exhibits progressively steeper and steeper fibers towards its posterior limit. These fibers are arranged in a fan-like manner along the tendinous raphe which gives off these fibers (figs. 21, 22, 24). In fact, this raphe gives off fibers at each side of its slope in a somewhat pinnate arrangement, but rather few issue from the anterior slope ($1b_{\beta}$). This

small hemipinnate group (β) inserts in a raphe-like ventral continuation of the above-described tendinous spur, which faintly splits portion 1b. We may call the spur B, and the more posterior raphe, which issues from the upper, knee-like angle between the "head" and the "body" of the quadrate from inside the posterodorsal temporal fascia, may be

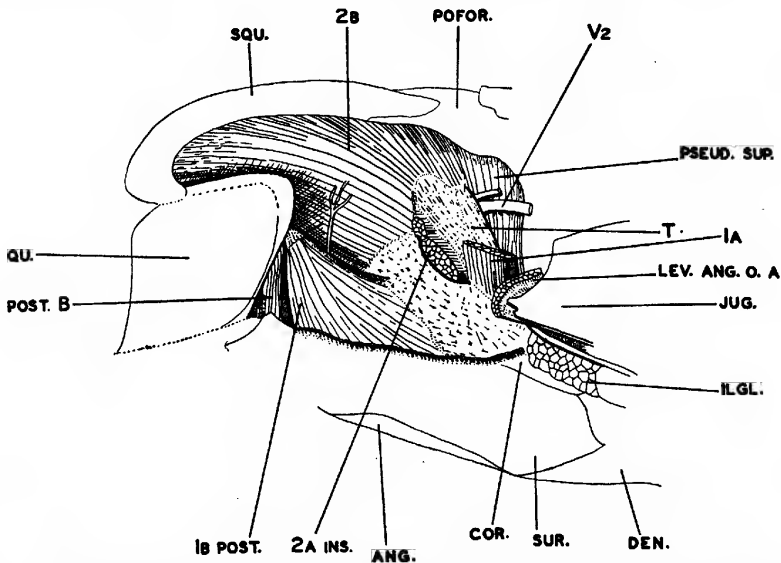


FIG. 26. *Shinisaurus*. 1b and 1b have been removed in order to show the full extension of 1b post. A great deal of 2a has been removed, with the exception of posteroventral insertions, showing their attachment on the lateral surface of a fascial sheet which forms the end of 2b and abuts the basal aponeurosis.

called raphe C. Were there not fibers linking C with B, we could speak of a clearly tripartite adductor externus superficialis. Such does not, in fact, exist, but is almost differentiated.

Raphe C gives off fibers externally in a bipinnate but asymmetrical arrangement (best seen in fig. 22), because the shorter, ventral anterior slope serves as insertion for ventrocaudal fibers of the cranial half of 1b. Part of the deeper and more caudal fibers rise from the inside of the external, posterodorsal covering aponeurosis above the quadrate, as the cranial 1b portion, and part from the ventrally bent hindmost part of the temporal arch above the upper articulation of the quadrate. The origo of this bipinnate caudal half of 1b (γ) is therefore rather complex, as it is linked anteriorly with the posterodorsal aponeurosis; more posterodorsally, with the bony frame above the quadrate and, by the aid of the tendinous raphe, with the caput quadrati. The most caudal inner bundles follow closely the anterior slope of the quadrate and end

at a slight prominence of the cranial border of the articular cavity of the articular bone (fig. 25), better considered as part of the adductor posterior (post. B, p. 31). This small bundle is completely covered by caudal fibers emerging from the raphe (fig. 24). The caudal part of 1b fills the trench of the compound bone laterally, following the rostral portion of 1b, which slightly overlaps the posterior portion by reaching, as mentioned above, ventral parts of the raphe. External fibers insert along the sharpened lateral osseous rim of the fossa primordialis mandibulae.

An uncontroversial homologizing of these and deeper adductor layers with Lakjer's portions of this muscle is extremely difficult owing to partial splittings and the rather uniform slope of all these subdivisions from posterodorsal to antero-ventral; this slope grows steeper towards the vicinity of the quadrate articulation. In *Sphenodon*, for instance, the very different directions of the various adductor portions facilitate a clear distinction of the different portions. Similar clear differences in fiber directions and a clear individualization of the normal portions prevail in the iguanid *Ctenosaura* (Oelrich, 1956).

Adductor Mandibulae Externus Medialis (2): After the removal of 1a and the complex 1b, a strictly bipartite medialis is exposed (2a, 2b, figs. 18, 22-25). The posterior contour of this muscle is clearly stressed by an emerging motor branch of the trigeminus, probably for the adductor externus superficialis. Both portions have a considerable share in filling two-thirds of the upper temporal opening: the lateral, smaller portion rises from the external circumference; the much larger, deep portion from the posterior border (fig. 18), filling the central area of the window as a craniad tapering field, the apex of which points somewhat anterolaterally. Both muscles converge towards the basal aponeurosis. The external portion (fig. 22) inserts at the lateral surface. The deeper portion, mostly hidden except for a narrow cranio-dorsal fraction, ends at the external and internal surfaces, respectively, of a tendinous expansion which converges in a rostroventral slope into the basal aponeurosis (figs. 25-27, T). The inner portion inserts, however, at a deeper level than the other. Figure 25 shows the external insertion at the posterodorsal corner of this aponeurosis. This insertion is caudal to high insertions of the cranial group of 1b, which covers, taken as a whole, the arched area indicated as a broken line in figure 25. In figure 26 the ventral, considerable development of the end aponeurosis of the posterior part of 1b (1b post.) is shown. This suggests a profundus laterally transposed; the insertion at the lateral surface of the aponeurosis explains the true nature of this portion.

The deep portion of the medialis has a very extensive origo from the "wing" of the parietal at the posterior and medial circumference of the temporal fossa and ends in a sloping tendinous ridge fused along the ventral border of the basal aponeurosis. Fibers rise also from the supratemporal where it is in contact with the wing of the parietal. The muscle keeps clear, however, of the inner (medial) surface of the parietal wing. The above-mentioned tendinous ridge of the basal aponeurosis delimits more or less the ventral border of the deep medialis; beneath this ridge, the long-fibered proötic caput of the profundus reaches the medial surface of the basal aponeurosis (3c, fig. 28).

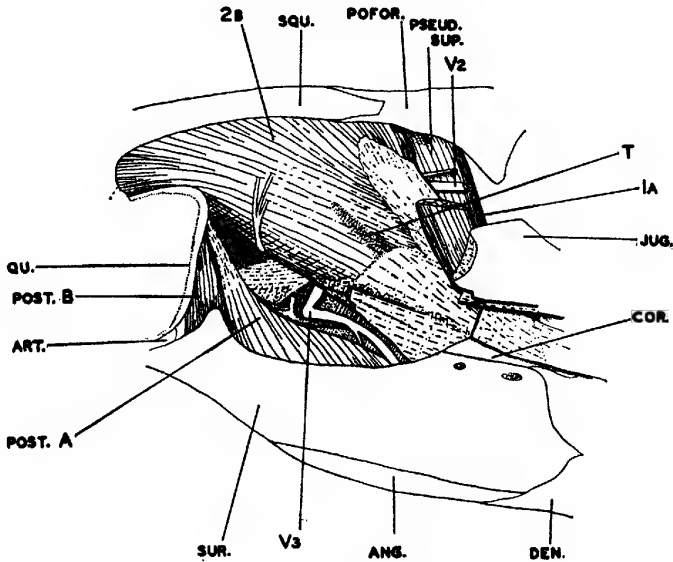


FIG. 27. *Shinisaurus*. After removal of 1b post., the anterior part of the adductor posterior (post. A) with its origo tendon is exposed. 2a has been completely resected. The stippled spur T indicates a tendinal internal ridge jutting from the insertional aponeurosis of 2b and collecting a number of deeper fibers of this portion. The knee-like bend of V3 emerges under the lower margin of 2b.

Adductor Mandibulae Externus Profundus: The deeper portions of the externus converge into a "basal aponeurosis," which does not fuse with the ventral part of the m. pseudotemporalis superior as it does in *Xenosaurus*. The main fiber direction of this muscle mass, taken as a whole, is a slope from its posterodorsal origins towards its ventromedial insertions. The slope is least along the anterior border and gradually steepens posteriorly near the quadrate. The areas of origo are these: (1) the anterior slope of the quadrate; (2) the region above the dorsal

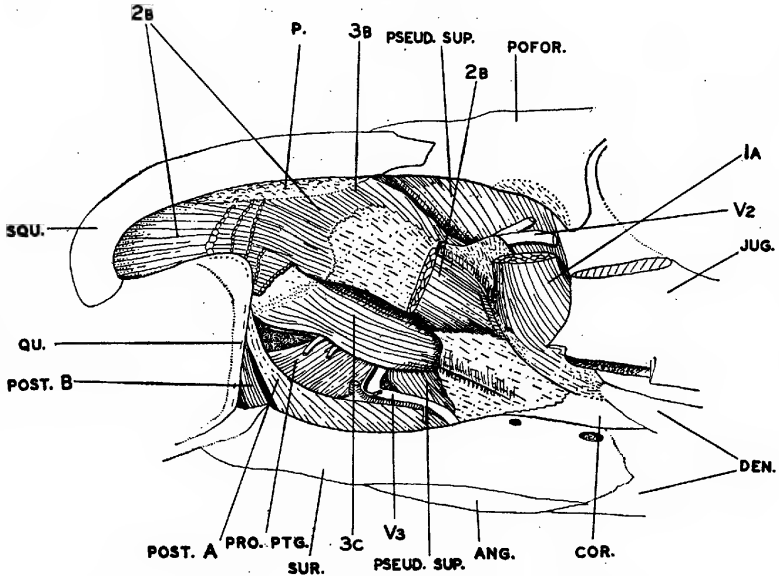


FIG. 28. *Shinisaurus*. Most of the deep medialialis (2b) has been removed. A considerable part of the basal aponeurosis has been bared. A portion, 3a, is not distinguishable. Inside the basal aponeurosis a typical portion, 3b (Lakjer), inserts. A separate proötic portion, 3c, is seen under the former. Perhaps 3a is fused with medial parts of 2b.

end of the quadrate, namely, the posterolateral end of the temporal arch (filling the corner between the ventrally recurved posterior end of the temporal arch and the upper border of the caput quadrati); (3) the posterior margin of the temporal fossa, as formed by the tabular and the upper and anterior face of the parietal wings; (4) the ventral parts of the posterior part of the lateral circumference of the fossa (the squamosal); and (5) the posterior border of the terminal lateral wings of the parietal (the 3b portion of Lakjer, which bulges into the post-temporal window). In addition, other origo areas cover the lateral surface of the proötic. The slight "descensus" of the parietal under the main level of the temporal fossa forms mainly a wide attachment area of this muscle group. Most of the resulting, more or less separable, profundus portions converge into the medial surface of the basal aponeurosis.

The basal aponeurosis collects a large array of parallel fibers at its inner surface, which represents the adductor externus profundus (3). This aponeurosis reaches the free ventroposterior margin of the parietal wing and in this way clearly separates the deeper profundus system from the parallel, but lateral, deep medialialis. After the removal

of this deep medialis, which, especially at the posterodorsal corner above the quadrate, is a very bulky and thick muscle, the extensive belly of the profundus is exposed (3b, fig. 28). Figure 29 shows the attachment of the basal aponeurosis at the ventral border of the parietal and the separation between the muscles in question.

The profundus rises from the medial surface of the parietal wing and forms a post-temporal muscular bulge. It corresponds, therefore, with Lakjer's 3b. Figure 28 also shows the confluence of the aponeurosis separating the two medialis portions with the basal aponeurosis, which bulges dorsal and ventral to the slanting plane of fusion. At the anteroventral process of the proötic wing, a small nerve perforates the proötic portion of the profundus (3c, fig. 29). Most of the fibers rise along the whole anterior and ventral border of the proötic, but a small deep bundle arises from the inner (medial) surface of this bone and fills the notch between the anterodorsal and the anteroventral processes, covering the Gasserian ganglion (the stump is seen at 3d, fig. 30). The long-

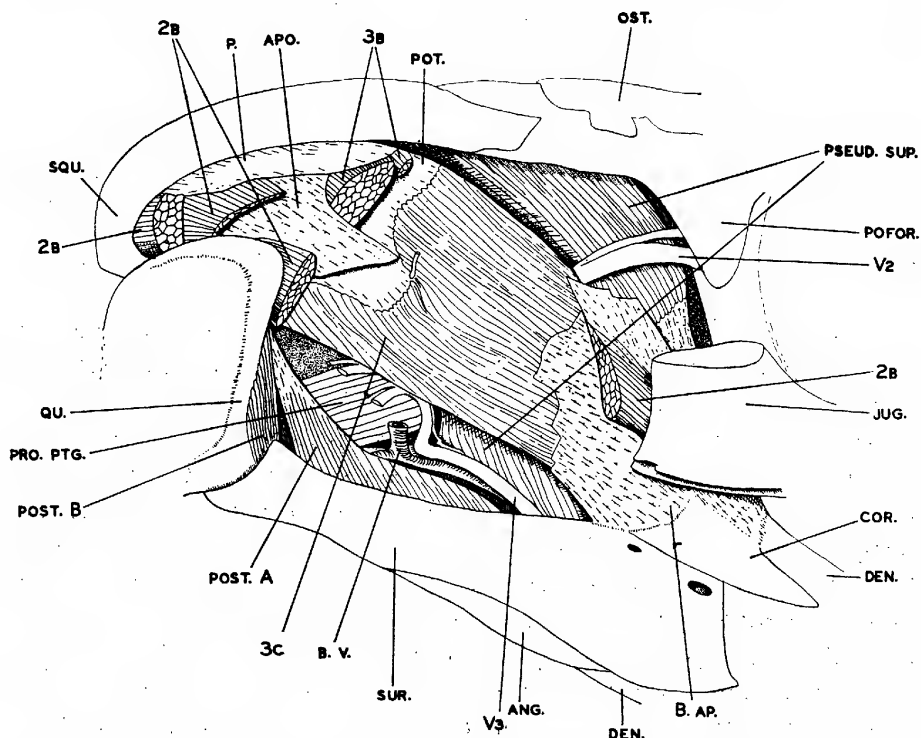


FIG. 29. *Shinisaurus*. Full view of 3c and of the aponeurosis (apo.) separating the deep medialis 2b from 3b which rises from the medial surface of the parietal wing. The pseudotemporalis superior is exposed near its insertion as well as the protractor pterygoidei (pro. ptg.).

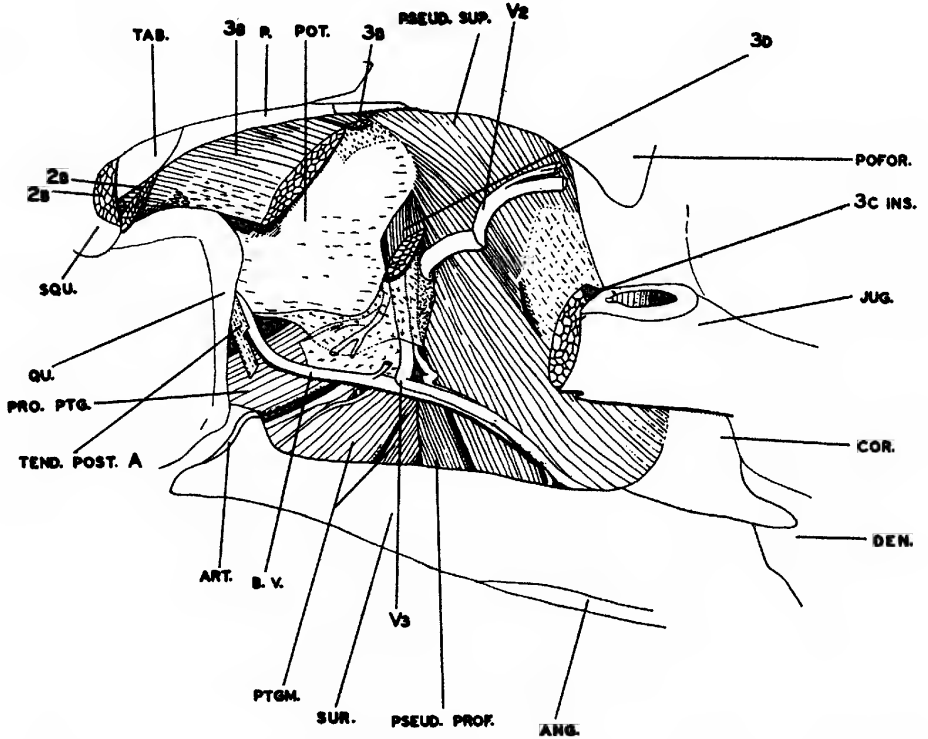


FIG. 30. *Shinisaurus*. 3b and 3c have been removed; the deepest portion 3d of the adductor externus profundus rises steeply from the anterior margin of the proötic. The bulky pseudotemporalis superior and the tendinous covering of V2 and V3 are exposed. Note the position of the m. pterygoideus.

fibred build of the proötic head of the profundus contrasts with the short-fibred arrangement of the post-temporal belly, with its extended insertional surface at the dorsal two-thirds of the basal aponeurosis.

We must emphasize the unusual, almost parallel, and very slanting course of both the medialis and considerable parts of the profundus. The combined pull of both muscles is transferred to the posterior margin of the coronoid bone. It may be assumed that the excessive development and slope of the medialis caused the enlargement of the basal aponeurosis and of the portion 3b. The same enlargement of the medialis caused perhaps a separation between lateral and medial profundus portions, if we should not see in the most caudal part of muscle 1b a laterally transposed part of the profundus, partly fused with the real 1b. The author favored such an explanation at one time, dismissed it later, and came to the conclusion that a real origo from the quadrate for the profundus must be excluded. Nevertheless, the secondary fusion with 1b remains a possibility but does not justify the separation under

a distinct name of the closely linked posterior parts of our 1b. The uncharacteristic form of the adductor posterior in *Shinisaurus* makes it possible that this small, bipartite muscle may (as indicated above, p. 31) in fact represent the quadratic belly of the externus profundus. It is, indeed, very arbitrary to ascribe the fibers rising from the anterior slope of the quadrate to different muscles which in fact gradually differentiate as we proceed in a cranial direction. The author acknowledges the weakness of this point in the description but could only stress the vagueness of the limits in the posteroventral temporal region.

CONSTRUCTOR INTERNUS DORSALIS SYSTEM

This muscle group shows a general resemblance and correspondence to that of *Xenosaurus*, but there are some differences in the relative size of the muscles and a few special divergences. The m. protractor pterygoidei is relatively less developed than in *Xenosaurus* (figs. 30, 31, pro. ptg.) and is faintly subdivided into two distinct fields of origin (fig. 32), but the insertion on the roof of the posterior part of the pterygoid bone forms a coherent longitudinal area. The rostral fibers rise from the basisphenoid flank, and this slightly smaller bundle consists of more slanting fibers than the posterior part, which rises from the anteroventral corner of the proötic wing, just posterolateral to the Gasserian ganglion (from the medial side of the proötic margin; see fig. 32). The bifid muscle develops, therefore, in front and behind the ganglion, the anterior part a little medial, the posterior a little lateral, to it. A triangular gap between the two portions gives room for the emerging ganglion. The steeper caudal part is slightly overlapped laterally by the anterior one. No such subdivision occurs in *Xenosaurus* in which almost the whole muscle descends from an area cranial to the ganglion Gasseri.

The m. levator pterygoidei as well is weaker than that of *Xenosaurus*. This whole muscle takes its origin from the anterior tip of the proötic wing, medial and caudal to the upper end of the epipterygoid (fig. 32, lev. ptg.), rising from the inner (medial) surface of the bone. The strict place of the origin is hidden from outside by a slanting tendinous band which links the anterodorsal with the anteroventral prominences of the proötic wing and which covers parts of the trigeminal ganglion. The anterior part of the strictly vertical fibers is hidden laterally by the epipterygoid. The narrow insertional field at the roof of the pterygoid is relatively shorter than in *Xenosaurus*, in which this muscle has an elongated origo in front of the proötic. These anterior parts of the muscle, almost two-thirds of its anteroposterior

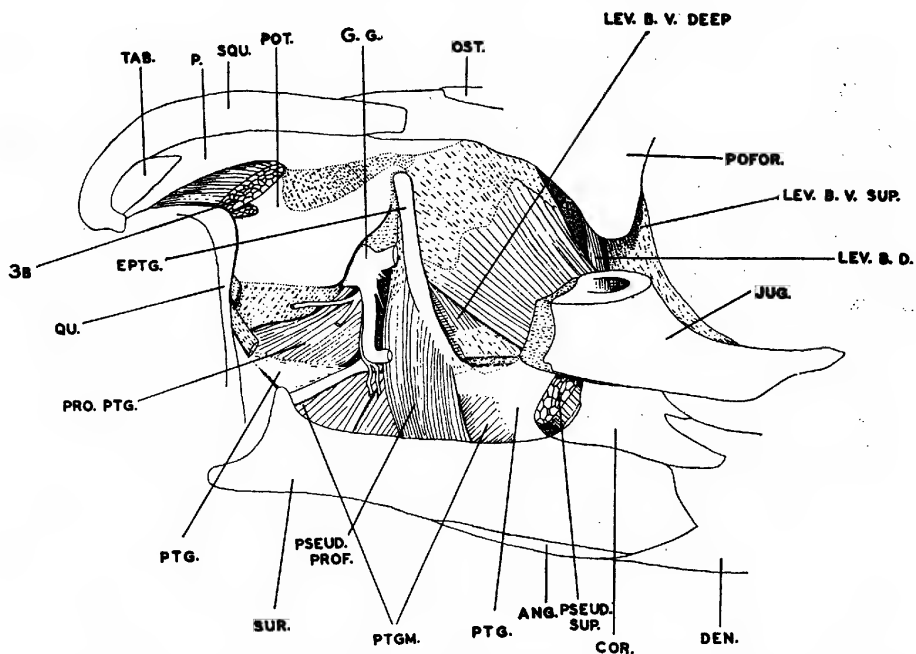


FIG. 31. *Shinisaurus*. The fleshy pseudotemporalis profundus (pseud. prof.) is visible after removal of the pseudotemporalis superior. A bifid levator pterygoidei and both parts of the levator bulbi [levator bulbi dorsalis (lev. b. d.) and levator bulbi ventralis (lev. b. v. deep and lev. b. v. sup.)] are seen.

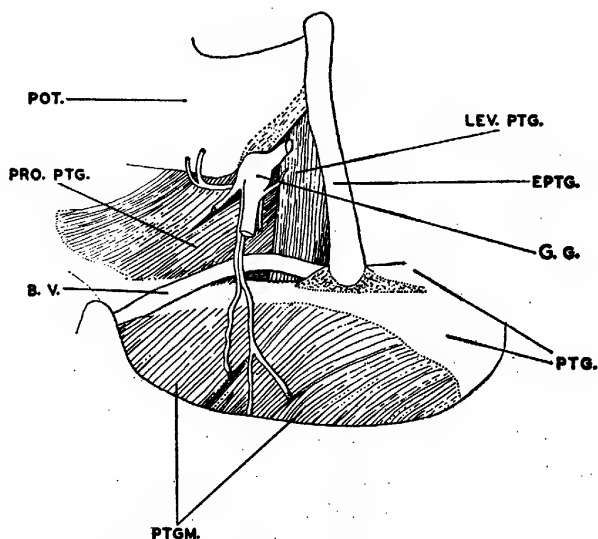


FIG. 32. *Shinisaurus*. Detail showing how parts of the deeper levator pterygoidei (lev. ptg.) penetrate into an area medial and caudal to the epipterygoid, rising from the inside of the proötic wing.

width, rise from the membranous lateral wall of the brain case; such a cranial anterior attachment is absent in *Shinisaurus*. The rather slight development of the above-mentioned muscles shows that pterygoid movements cannot be considered in this form; the whole arrangement provides more for an elastic fixation of the palatal bones than for a motile kinetic apparatus.

The levator bulbi group of *Shinisaurus* differs from that of *Xenosaurus* in one main point: the caudal muscle, the levator bulbi ventralis, which is single and rather feebly developed in *Xenosaurus*, is subdivided in *Shinisaurus*. There is a fairly extensive anteroposterior area of origin (fig. 31, lev. b. v. sup.) from the membranous wall of the brain case. In addition, a deeper, short-fibered, caudomedial portion (lev. b. v. deep) emerges medial to and in front of the lower end of the epipterygoid and ends on the palatal membrane. The origo of this deep portion is hidden by the much more extensive lateral portion, the fibers of which, converging fanwise towards the roof of the palate, have a steeper slope at the anterior end, thus almost parallel with the inner muscle, but have a very slanting course at the posterior margin. The origin from the brain case wall follows a wavy line of attachment with three prominences. As in *Xenosaurus*, an isolated portion of the levator bulbi descends from the inside of the postorbital bar and disappears in an almost vertical direction, medial to the anterior border of the levator bulbi ventralis (fig. 31, lev. b. d.). This portion, the levator bulbi dorsalis, probably rises from the under side of the suture between the postfronto-postorbital with the parietal, but its lower part could not be followed without destroying the skull. Probably this muscle swings forward as a tendon, encompassing the bulbus oculi from behind and below.

The main difference between the genera in respect to this muscle group lies in the strong development of the bipartite levator bulbi ventralis in *Shinisaurus*, combined with a very weak levator pterygoidei, which is restricted to a slim band caudal to the epipterygoid. In *Xenosaurus* the levator pterygoidei is very much expanded into regions in front of the epipterygoid. This condition probably restricts the origin of the single levator bulbi ventralis to a short area. The protractor pterygoidei in *Shinisaurus* shows by its subdivision into two distinct parts a slight deviation from a more common arrangement. The little levator bulbi dorsalis is virtually identical in both genera.

DISCUSSION

Our knowledge on the differentiation of the jaw muscles in saurians is, in view of the huge number of species, rather meager. Since Lakjer's

publication in 1926, Lubosch (1933) has covered a related field, but concentrated also on the facialis group. The recent papers by Poglayen-Neuwall on *Hatteria* (= *Sphenodon*) (1953a) and crocodiles (1953b), as well as Oelrich's beautiful description of the anatomy of the head of *Ctenosaura*, are welcome additions for an understanding of saurian conditions. An important new item concerning *Sphenodon* is the existence of a levator anguli oris in this form. This muscle is therefore not a purely saurian differentiation, although lacking in crocodiles and birds. All diapsidian forms show in a convincing way that the lower temporal arch (horizontal wing of the jugal, the quadratojugal, and parts of the squamosal) is, with the exception of the levator anguli oris in *Sphenodon*, devoid of muscular origins. The loss of this arch would therefore not alter basically a primitive arrangement derived from a diapsidian source. Our question is centered on the discussion of deeper differences between *Sphenodon* and the saurian type (excluding forms with a reduced, or secondarily narrowed, upper temporal arch). The Amphisbaenidae, Geckonidae, and Pygopodidae would not contribute to our problem, but the Agamidae, Chamaeleonidae, Teiidae, Iguanidae, and Varanidae have a well-developed upper temporal fenestra as do the forms described in this paper. Reduced upper temporal openings like those of the Lacertidae or Anguinae (*Ophisaurus*) are not very useful in this respect.

The first difference between saurians and *Sphenodon* concerns the levator anguli oris. It originates from the upper temporal arch instead of from the lower as in *Sphenodon*. A transmigration across the tendon-covered lower temporal opening must therefore be surmised as having taken place *pari passu* with a reduction of the temporal arch. In *Sphenodon* two muscles enter the upper temporal opening, the m. pseudotemporalis superior (cranially) and the adductor externus medialis (caudally). In this respect, *Calotes emma* shows the identical condition (Lakjer). In *Uromastix* and *Phrynosoma*, only the medialis bulges into the upper opening, whereas Lakjer shows that in *Tropidurus hispidus* the adductor externus superficialis (1b) shares the space caudally with an enormously expanded pseudotemporalis superior.

In *Ctenosaura*, as in *Calotes*, the adductor externus medialis and the pseudotemporalis superior are exposed. Among the forms studied here, *Shinisaurus* conforms to this pattern, whereas *Xenosaurus* has the whole area virtually filled by a huge adductor externus medialis alone. Other details concerning the extremely variable conditions that result from subdivisions and fusions in the area of the adductor externus are dealt with below.

The constrictor internus dorsalis system is of special interest, as this group of muscles is connected both with the eye and with the palatopterygoid complex. The second attachment causes the kinesis of certain reptile skulls. As a rule, an akinetic skull preserves the anterior portion, the levator bulbi group only, and the muscles linking the lateral wall of the brain case with elements of the palatopterygoid complex (including the epipterygoid and quadrate) are reduced or missing. Kineticism is virtually absent in *Sphenodon*, which shows an interesting stage of regression in the caudal group. According to Poglayen-Neuwall, a levator pterygoidei of minute dimensions is present, but there is no protractor pterygoidei.

No traces of the posterior group of the constrictor internus dorsalis system are found in the akinetic Crocodilia and Testudinata.

The richest differentiation of the cranio-ptyerygoideal muscles occurs in the highly kinetic snakes, in which two muscles, the retractor pterygoidei and the retractor quadrati, are added to the normal protractor and levator muscles. The protractor especially can attain a considerable bulk. Lakjer sees in both "new" muscles of the snakes transformed portions of the levator bulbi ventralis, as no other muscles representing the retractor bulbi group occur in snakes. As a further complication, a posterolateral part of the protractor pterygoidei connects with the ventromedial part of the quadrate in some highly streptostylic snakes (certain colubrids and solenoglyphs). Even in snakes many special differentiations in this deep muscle group can be found. The size and bulk of these muscles are a good guide for an estimate of the degree of kineticism. Special conditions occur in the Leptotyphlopidae, which appear to represent the only group of snakes without a trace of a levator pterygoidei (at least in *L. maxima* and *L. macrolepis*). In typhlopids, the protractor and retractor are strongly developed, and the massive levator (Haas, 1930) has been transformed into a retractor maxillae by a shift of its insertion from the palatopterygoid chain onto the maxillary. I prefer this interpretation of the muscle to that of Lakjer, who based interpretation on innervation. His scheme is untenable, owing to a "barrier" in the form of the course of the main mandibular branch of the trigeminal. As "adductor posterior," this muscle by definition must pass dorsolateral to this nerve. According to Lakjer, the Anilidae have no retractor vomeris. In saurians, both the levator bulbi, in typical connection with the eye and the orbital region, and the levator and protractor are developed. Rarely, the levator may be reduced (*Calotes*; Lakjer), but the protractor is always present, though in different degrees of development.

In details, the levator bulbi group shows a variety of differences from the forms considered in this paper (compare also the discussion in Lakjer, 1926, p. 15). It is strange that in *Ctenosaura* this group is represented by only one weak portion (Oelrich, 1956), whereas other iguanids (*Iguana*) show an astonishing degree of complexity, even surpassing Lakjer's subdivisions (levator bulbi dorsalis and ventralis). The ventral portion corresponds with the retractor pterygoidei of the Ophidia. In *Xenosaurus* and *Shinisaurus* there is a very small levator bulbi dorsalis, originating from the under side of the "root" of the postorbital bar (suture between p. and pofor.). In these genera this portion and the levator bulbi ventralis seem to end at the palatine membrane exclusively. But in *Shinisaurus* the lower muscle is bipartite. A more lateral and larger portion is continued towards the bulbus, and a steep-fibered, smaller levator bulbi ventralis agrees with the single ventral part of *Xenosaurus* in ending at the palatine membrane. The single muscle of the levator bulbi group in *Ctenosaura* corresponds fairly well with this levator bulbi ventralis of *Xenosaurus*. The fact that among closely related genera of iguanids one genus should possess a richly differentiated levator apparatus for the bulbus oculi and the other not is very remarkable and certainly points to significant differences in the motility of the eyelids.

The adductor mandibulae internus group (according to Lakjer's definition) has a high degree of constancy in all saurians. Only slight differences in relative size obtain for the very characteristic m. pterygoideus, though an extraordinary expanded superficialis and profundus portion characterizes *Uromastix*, according to Lakjer, and various conditions of more or less gradual fusion or clear separation are described. In *Ctenosaura* the muscle is considered as an entity ("pterygomandibularis") without clear subdivisions, but divisions may occur easily. As a whole, however, the external shape and position of origo and insertion make this muscle the most characteristic of the adductor series. In *Sphenodon* this muscle is described as undivided by Lakjer, but Poglayen-Neuwall (1953a) mentions an accessory "portio atypica," which, well separated from the latter, inserts at the anterior ridge of the coronoid process and rises from the roof of the palatine and the ventral part of the septum inter-orbitale in the region of the bulbus oculi. Both forms described here follow the normal scheme. The "*Kauballen*" is modestly developed in both forms, and a sharp subdivision does not occur. The second part of the adductor mandibulae internus, the pseudotemporalis, is always present in saurians. Its position medial to the V2 defines clearly the boundary from the externus group. Two

main conditions can be distinguished: the muscle may be single, or it may be clearly bipartite. The second condition, found as well in *Sphenodon* and in crocodilians and birds, seems to constitute the normal arrangement. Lakjer describes several cases of a partial fusion but mentions only *Phrynosoma*, *Lygosoma*, the Geckonidae, and the Pygopodidae as preserving only the deeper portion (pseudotemporalis profundus). Only a single and fairly simple muscle is found in all families of ophidians. In both forms dealt with here the normal double pseudotemporalis is found. In *Shinisaurus*, the pseudotemporalis profundus is a fleshy, shortened muscle rising only from the two ventral thirds of the epipterygoid. The lateral pseudotemporalis superior is, in contrast, a very bulky muscle, not fused with the dorsal aponeurosis of the adductor externus profundus. Only the anterolateral slope forms a tendinous sheet. Among Lakjer's figures, no parallel with this peculiar reduction of the pseudotemporalis profundus could be found.

In *Xenosaurus*, a moderate pseudotemporalis superior ends mainly at the medial surface of a tendinous complex rising from the posterior slope of the coronoid elevation and, as a deeper lamina, joins the basal aponeurosis cranioventrally. Most of the temporal surface of the muscle is fleshy, and in this way the most cranial fibers reach directly to the summit of the coronoid process. The truly enormous pseudotemporalis profundus envelops the epipterygoid, rising from the proötic wing above the upper end of the epipterygoid. In its narrow origin from the proötic distal extension and its entirely fleshy, long-fibered composition it reminds one somewhat of the condition found in *Phrynosoma* (Lakjer, 1926, fig. 166). It is worth while to stress the relatively short junction with the real dorsal aponeurosis, very close to the common insertional ridge. *Zonurus* (= *Cordylus*) (Lakjer, 1926, fig. 164) and *Chamaeleon* (Lakjer, 1926, fig. 173), according to the figures, seem to have abolished any aponeurotic structures, and a long-fibered double muscle (the pseudotemporalis superior being minute) is present.

The striking differences between *Shinisaurus* and *Xenosaurus* in this muscle group, in spite of so many other common features, should be emphasized, as well as the differences in the invasion by parts of the pseudotemporalis of the upper temporal opening (not in *Xenosaurus*; partly in *Shinisaurus*).

The genera conform in having an ill-defined adductor posterior, or even no such portion at all. Perhaps, though it is very doubtful, our 3c in *Xenosaurus* may represent this muscle, as may the deep, fan-shaped muscle rising from the inner anterior corner of the upper quadrate head in *Shinisaurus*.

The first assumption seems too far fetched. An adductor posterior could not reach the system of the dorsal aponeurosis and overlap the ventral part of the pseudotemporalis over such a broad area.

The fairly cranially situated exit of the V3 and the cranially bent course of it towards the mandible preclude an overlapping of caudal adductor portions by this nerve. Therefore the interpretation of innermost and caudal adducent fiber systems (rising from the quadrate) as an adductor posterior must remain doubtful. No adductor posterior portions truly medial to the V3 occur in the genera in question.

A fairly well-developed adductor posterior is described in *Sphenodon* by Poglayen-Neuwall and Lakjer; that this muscle forms a caudal extension of the pseudotemporalis profundus probably represents a primitive condition.

The adductor mandibulae externus, subdivided by Lakjer into three main parts, exhibits in the saurians such a high degree of variation in form, number, and position of its parts that every attempt to understand this multiplicity of differentiation in relation to the construction of the skull as a functional unit seems hopeless. We mention above the "fourth" adductor portion in the form of a levator anguli oris, recently found in *Sphenodon* as well. The two forms discussed and described in this paper exhibit an adductor mandibulae externus in a fairly typical form. A detailed comparison of the separate adductor portions would not be worth while; both genera have in common a very complex array. Many tendinous spines and blades blur even the original tripartite arrangement in *Xenosaurus*, a form with a fairly broad and flattened skull. Such a condition contrasts sharply with that in *Shinisaurus*, the skull of which has a rather high build. Both are similar in having a well-developed upper temporal fenestra. In both forms, most of the deeper adductors have a fairly slanting course. Only the lateral portions are steeply fibered. All the deeper adductors seem to be centered around a field of origin delimited by the caudal and posteromedial part of the temporal fossa and the area between the dorsal head of the quadrate and the outer border (and under side) of the hind portion of the upper temporal arch. This general tendency to a scarcity of vertical adducent fiber systems is even more striking in the outer adductor layers of *Xenosaurus*. In accord with this main arrangement, the posterior slope of the coronoid process rather than the summit of this prominence is the main insertional field. Thus the powerful profundus system in *Shinisaurus* is more a retractor than an adductor mandibulae. Studies *in vivo* concerning the chewing of these forms could perhaps further our insight about this peculiar predominance of a retracting

pull on the mandibular articulation. Could it be a safeguard against exarticulation of a moderately buttressed jaw articulation endangered by a struggling prey?

Shinisaurus has a stronger tendency to transform deeper insertional parts of the adductor system into aponeuroses and fiber-catching tendinous sheets or spines. All these structures converge into a common insertional area of fairly reduced extent.

The slanting course of all the deeper adductors blurs the primary tripartite arrangement of this muscle group and makes a clear delimitation of a medialis almost impossible.

The superficial throat muscles of both genera refer them clearly to Camp's Anguioidea. The similarity between *Xenosaurus* and *Shinisaurus* is very striking in this respect (see also p. 26). Especially the presence of a separate geniomyoideus should be mentioned. The geniohyoideus is rather simple and does not show the lattice-like interdigitations with the mylohyoideus anterior and posterior, a feature so prominent in scincomorphs. As in *Xenosaurus*, the mylohyoideus is divided into four clearly discernible systems in *Shinisaurus*.

SUMMARY

The superficial layers of the throat musculature in *Xenosaurus* and in *Shinisaurus* are very similar in respect to both the differentiation and the arrangement of the constituent portions. In the case of *Shinisaurus*, the similarity with *Xenosaurus* places the former clearly in Camp's group Anguioidea.

The detailed comparison of the trigeminus musculature, however, shows some remarkable differences between both forms.

In both genera the upper temporal opening is wide, but the skull as a whole is rather flattened and broad in *Xenosaurus*, high and narrow in *Shinisaurus*. This difference is accentuated in the temporal area, the space in which most of the temporal muscles are situated.

Both forms possess a levator anguli oris muscle, which is not always found in saurians and ophidians.

The m. adductor mandibulae externus is extremely complex, and its often assumed (Luther, Lakjer) tripartite arrangement is blurred in many ways. Especially the boundary between the medialis and profundus portion of this muscle group is not easily determinable owing to partial fusions and parallel fiber course in certain areas of contact.

Lakjer's "*Bodenaponeurose*" is not very extensive in either form. The existence of an adductor posterior remains very doubtful, but deepest parts of the m. adductor mandibulae externus profundus may

assume the position and the fiber arrangement of a real adductor posterior. The ramus mandibularis trigemini in its course towards the lower jaw does not overlap any deep adductor portions in such a way that would clearly separate the lateral profundus area from the medial adductor posterior component. In spite of this fact, deepest, well-separable parts of the profundus group could well represent parts of an adductor mandibulae posterior.

Owing to the fact that relatively few saurians have been thoroughly investigated as far as the trigeminal musculature is concerned, it is still too early to try to understand the intricate patterns of differentiation, especially of the m. adductor externus in connection with the morphological aspect of the skull and with phylogeny.

The deeper trigeminal muscles, otherwise of a fairly constant arrangement, differ strikingly in both forms under consideration.

Both portions of the m. pseudotemporalis exhibit a certain degree of correlative development: both muscles together are of a corresponding volume in relation to the mass of the other adductors. But in *Shinisaurus* the m. pseudotemporalis superior is the bigger of the two muscles of this group, whereas in *Xenosaurus* the profundus portion is the prevalent one.

Both genera, owing to a certain degree of cranial kineticism, exhibit mm. protractores and levatores pterygoidei. The protractores are fairly similar but are slightly better developed in *Xenosaurus*. The levator pterygoidei is weak and almost not retrahent in both forms—really a “levator” only. The levator bulbi ventralis is bipartite in *Shinisaurus*, single in *Xenosaurus*.

Ophisaurus, the only other anguid of which the trigeminal musculature has been studied, has, in contradistinction to both forms dealt with in this paper, a very narrow temporal opening. This fact alone has a deep influence on the arrangement and the differentiation of the jaw muscles. In forms with large temporal openings parts of certain temporal muscles bulge into this opening in very different patterns. Parts of the mm. adductores externi superficiales and/or mediales, and/or the m. pseudotemporalis superior, may be involved. Very often, the single or bipartite adductor externus medialis fills the opening exclusively, but other combinations may occur as well. The significance of these different penetrations into the temporal opening is so far not understood, in spite of the fact that the arrangement of the temporal arches in sauropsids constitutes one of the main systematic criteria. So both forms discussed here differ in respect to the muscular penetrations into the wide temporal openings. In *Shinisaurus*, the m. pseudotem-

poralis superior shares the temporal aperture with a bipartite m. adductor externus medialis, as in the agamid *Calotes* or, in somewhat different distribution of the muscular shares involved, as in *Sphenodon*, in which the medialis is single. In *Xenosaurus*, however, the two portions of the m. adductor externus medialis fill the temporal fenestra exclusively, as in the agamid *Uromastix*, the iguanid *Phrynosoma*, and *Chamaeleon*, representing a separate group, probably connected with the Agamidae or with both the Agamidae and Iguanidae.

BIBLIOGRAPHY

BARROWS, S., AND H. M. SMITH

1947. The skeleton of the lizard *Xenosaurus grandis* Gray. Univ. Kansas Sci. Bull., vol. 31, pp. 227-281, pls. 11-16.

CAMP, C. L.

1923. Classification of the lizards. Bull. Amer. Mus. Nat. Hist., vol. 48, pp. 289-481, figs. 1-112.

EDGEWORTH, F. H.

1935. The cranial muscles of vertebrates. Cambridge, Cambridge University Press, 493 pp.

HAAS, G.

1930. Über das Kopfskelett und die Kaumuskulatur der Typhlopiden und Glauconiiden. Zool. Jahrb., vol. 52, pp. 1-94, figs. 1-127.

LAKJER, T.

1926. Studien über die trigeminus-versorgte Kaumuskulatur der Sauropsiden. Copenhagen, Reitzel, pp. 1-15, pls. 1-26.

LUBOSCH, W.

1933. Untersuchungen über die Visceralmuskulatur der Sauropsiden. Morph. Jahrb., vol. 72, pp. 584-663.

LUTHER, A.

1914. Über die vom N. Trigemini versorgte Muskulatur der Amphibien. Acta Soc. Sci. Fennicae, vol. 41, pp. 43-120.

MCDOWELL, S. B., JR., AND C. M. BOGERT

1954. The systematic position of *Lanthanotus* and the affinities of the anguimorph lizards. Bull. Amer. Mus. Nat. Hist., vol. 105, pp. 1-142, figs. 1-43, pls. 1-16.

NOPCSA, F.

1932. Zur systematischen Stellung von *Shinisaurus*. Zool. Anz., vol. 97, pp. 185-187.

OELRICH, T. M.

1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Misc. Publ. Mus. Zool., Univ. Michigan, no. 94, pp. 9-122, 59 figs.

POGLAYEN-NEUWALL, I.

- 1953a. Untersuchungen über die Trigemini-muskulatur von *Hatteria*. Zeitschr. Wiss. Zool., vol. 157, pp. 57-76.
1953b. Untersuchungen der Kiefermuskulatur und deren Innervation in Krokodilen. Anat. Anz., vol. 99, pp. 257-276.

SÄVE SÖDERBERGH, G.

1945. Notes on the trigeminal musculature in non-mammalian tetrapods. *Nova Acta R. Soc. Sci. Upsaliensis*, ser. 4, vol. 13, no. 7.

UNDERWOOD, G.

- 1957a. *Lanthanotus* and the anguinemorphan lizards. A critical review. *Copeia*, pp. 20-30.
- 1957b. On lizards of the family Pygopodidae. A contribution to the morphology and phylogeny of the Squamata. *Jour. Morph.*, vol. 100, pp. 207-268, figs. 1-11.